Landscape heterogeneity affects arthropod functional diversity and biological pest control

Dissertation
to obtain the Ph. D. degree
in the International Ph. D. Program for Agricultural Sciences in Goettingen (IPAG)
at the Faculty of Agricultural Sciences,
Georg-August-University Göttingen, Germany

presented by

MSc. Ing.
Aliette Bosem Baillod
born in Basel, Switzerland

Göttingen, December 2016

“ The most unique feature of Earth is the existence of life, and the most extraordinary feature of life is its diversity ”
Cardinale B. J. *et al.* 2012,
Biodiversity loss and its impact on humanity, Nature (59)

D7

1st supervisor: Prof. Dr. Teja Tscharntke

2nd supervisor: P.D. Dr. Yann Clough

3rd supervisor: P.D. Dr. Péter Batáry

Date of thesis submission: 22 December 2016

Date of dissertation: 1 February 2017

TABLE OF CONTENTS

SUMMARY

Land-use change is a major cause of biodiversity loss. In agricultural landscapes, which cover 40% of European land, changes in land-use are spatially and temporally very dynamic, thereby changing the organisms' habitat availability. In the last decades agriculture has been intensified through (1) shortening of crop rotations and smaller numbers of crops grown, (2) enlargement of cultivated fields and (3) loss of semi-natural habitats such as hedgerows or grassy strips. This resulted in loss of spatial and temporal heterogeneity of cropland. The spatial heterogeneity of crops can be described by two components: the diversity of crop types (compositional heterogeneity) and the spatial arrangement of cultivated fields (configurational heterogeneity) in the landscape. The temporal heterogeneity represents changes in crop composition due to annual crop succession. In intensified and dynamic landscapes, biodiversity plays a crucial role in sustaining environmental sound food production. Indeed, farmland biodiversity fulfils important ecosystem services such as biological pest control. For example, predatory arthropods such as carabid beetles and spiders can regulate pest outbreaks. Loss of species and functional diversity can have negative consequences on ecosystem services. While it is well known that semi-natural habitats interspersed within cropland enhance beneficial arthropods and associated services, there is no evidence that the heterogeneity of crops in space and time supports them.

The **first and second part** of this thesis present results from a pan-European and Canadian study analysing species diversity response to compositional and configurational heterogeneity. We selected 435 landscapes within five countries (Spain, France, U.K., Germany and Canada) along orthogonal gradients of increasing crop diversity (compositional heterogeneity) and increasing field border density (configurational heterogeneity). In each landscape, we sampled bees, hoverflies, carabid beetles, spiders and we monitored butterflies and birds in crops commonly grown in the regions. We showed for the first time that higher crop configurational and compositional heterogeneity can enhance carabid beetles, spiders, hoverflies, birds and plants diversity, while wild bees remained unaffected and configurational heterogeneity negatively affected butterflies diversity. Further, in the second part we showed that generalist predators (carabid beetles and spiders) and flower-visitors (butterflies and hoverflies) species traits responded to cropland heterogeneity in cereal fields across the four European countries. We found that landscapes with more crop diversity favoured spider species that live both in soil and vegetation strata and hoverflies with low reproductive potential. Landscapes with more field borders (smaller field on average) selected for specialised feeders of carabid beetles and butterflies. This is likely to have consequences on ecosystem services such as pest biological control and pollination provided by generalist predators and flower-visitors. Such cascading effects are further investigated in the next part of the thesis.

In the **third part**, we explored the cascading effect of landscape crop heterogeneity and generalist predators' functional diversity of communities (carabid beetles and spiders) on biological pest control. We estimated biological control potential as the predation rates of aphids added into the same cereal fields as described above. The biological control potential was positively affected by crop composition and carabid abundance. Landscape crop diversity had a positive effect on the biological control potential, but the effect became negative at higher crop diversity levels. Furthermore, carabids communities dominated by omnivorous species enhanced biological control. However, this diet trait was not affected by landscape crop heterogeneity. Spider abundance was positively affected by higher field borders in the landscape (smaller field on average), while communities shifted to smaller species with smaller field sizes. These results show that landscape crop heterogeneity and ground-dwelling arthropods' community traits affect biological pest control, though landscape effects are not mediated by communities' traits.

In the **fourth part**, I examined crop heterogeneity effects on cereal aphid pests, predators and pest control with a focus on spatial and temporal changes in the landscape. On a subset of cereal fields in the Göttingen region in Germany, we monitored live aphids, parasitized aphids and their vegetation-dwelling enemies (e.g. hoverfly larvae). Only aphids and their parasitism were affected by both spatial and temporal crop heterogeneity. Aphid infestation decreased in landscapes with higher crop diversity when land cover of aphid resource habitats (cereal, maize and grasslands) had decreased compared to the year before. Aphid control through parasitism decreased with the inter-annual expansion in aphid host habitat, but only in landscape with small field size. These results show that pest infestation can be reduced by higher crop heterogeneity in the landscape in space and time.

Focusing on the Göttingen region in Germany, I further explored in the **fifth part** the effect of crop heterogeneity on carabid beetle inter-specific (at community level) and intra-specific body size traits (within three species). Landscape crop diversity decreased the community's average body size in oilseed rape crops, while smaller-field landscapes decreased community's average body size but increased body size of the omnivorous beetle *Poecilus cupreus* in cereal crops. These results suggest that not only communities' structure can be affected by the spatial crop heterogeneity, but within-species trait variation as well.

Overall, I conclude that landscape-wide crop heterogeneity should be considered if we want to maintain and enhance agro-biodiversity and associated ecosystem services. We show for the first time that loss of crop heterogeneity or landscape homogenisation may (1) have negative consequences on species diversity, (2) favour generalist species over species with more specialized requirements and (3) reduce biological pest control. Likewise, inter-annual increase in land cover of one particular crop hosting pests can promote pest densities. This is a further argument to halt the expansion of monoculture or short crop rotations. Thus, we recommend that future landscape management strategies in Europe encourage both crop diversification and small-scale farming to sustain important ecosystem services.

INTRODUCTORY CHAPTER

Introduction

In Europe, agricultural intensification during the last decades caused high losses of biodiversity and related ecosystem services. Drivers of these losses operate at the field and landscape scale (Tscharntke *et al.* 2007; Geiger *et al.* 2010). Intensive use of pesticides at the field scale and the homogenisation of landscapes through (1) removal of semi-natural areas (e.g. hedges, grassy strips), (2) shortening of crop rotations and smaller numbers of crops grown and (2) enlargement of cultivated fields are the major causes of biodiversity declines (Benton, Vickery & Wilson 2003; Firbank *et al.* 2008; Stoate *et al.* 2009). Important ecosystem services, benefiting agricultural production such as biological control of pests, are therefore threatened (Tscharntke *et al.* 2007). In landscapes having large shares of semi-natural areas, biodiversity and biological control are often enhanced compared to landscapes with a high crop shares (Benton, Vickery & Wilson 2003; Chaplin-Kramer *et al.* 2011). In agricultural landscapes, semi-natural habitats provide important resources for species during their life-cycle and act as refuges from highly disturbed habitats such as crops (Bianchi, Booij & Tscharntke 2006). However, the effects of changes in cultivated areas such as simplification of crop rotation and enlargement of fields are often disregarded (Fahrig *et al.* 2011). Cultivated areas undergo regular disturbances and changes in space and time due to crop rotation. Therefore, this agricultural matrix is often considered as the least favourable habitat for dispersing and resident organisms (Tscharntke *et al.* 2012). However, cultivated areas have high biodiversity potential (Altieri 1999; Fahrig *et al.* 2011). Many species use crops as resource habitats during different stages of their lives. For example, generalist predators such as carabid beetles use crops for reproduction and to search for preys (e.g. Holland 2002) and wild bees forage in crops providing nectar (e.g. Westphal, Steffan-Dewenter & Tscharntke 2009). Cultivated areas may therefore be important for the provision of resources for organisms and are likely to have consequences on biodiversity and ecosystem services (Fahrig *et al.* 2011).

It has been recently suggested that biodiversity and ecosystem services can be enhanced in agricultural landscapes with spatially heterogeneous crop patterns (Fahrig *et al.* 2011). Landscape-wide crop heterogeneity encompasses a compositional and a configurational component. The compositional crop heterogeneity can be defined as the diversity of crops in a landscape. The configurational crop heterogeneity can be defined as the spatial arrangement of crops, which can be measured as mean field size or the density of field borders (Fig. I1). A crop diverse landscape may provide several resources for organisms and small-field landscapes increase the interspersion between crops, both factors leading to landscape complementation (Dunning, Danielson & Pulliam 1992). Although compositional and configurational heterogeneity of crops have been seldom teased apart, some recent studies reported mixed effects on biodiversity. For example, crop diversity and small-field landscapes have neutral or positive effect on diversity of several taxa (Fahrig *et al.* 2011; Palmu *et al.* 2014; Bertrand, Baudry & Burel 2016). In addition to the spatial crop heterogeneity, the temporal changes due to crop successions may influence biodiversity and biological control as well. For example, carabid beetles species richness benefit from increasing crop diversity over several years (Bertrand, Burel & Baudry 2016) and biological control decrease when the cover of prey-hosting crops increase inter-annually (Thies, Steffan-Dewenter & Tscharntke 2008).

However, the extent to which species respond to crop heterogeneity changes in the landscape may depend on their traits (Fahrig *et al.* 2011; Tscharntke *et al.* 2012). Species have different characteristics and requirements throughout their lives. Changes in the landscape can select species that have characteristics to cope with these changes. Landscape shapes therefore the assemblage of communities (Henle *et al.*, 2004; Tscharntke et al., 2012). As an example, homogenous landscapes characterised by low habitat diversity and high patch size favour generalist species over species with more specialised feeding habits and smaller body sizes (Gámez-Virués *et al.* 2015). Species also provide different functions in ecosystems, thus changes in communities are likely to affect functions and ecosystem services. For example, communities dominated by spiders with a preference for arable land and small body sizes increase biological control of aphids (Rusch *et al.* 2015). However, the link between landscape-wide crop heterogeneity, species traits and the consequences on biological control has not been investigated to date.

In this thesis, we investigated the effects of the spatial crop compositional and crop configurational heterogeneity on the diversity of carabid beetles, spiders, butterflies, hoverflies, bees, birds and plants across Europe. In addition, we examined the effect of temporal change in crops on aphid pests and their natural enemies. We further focused on the effect of the spatial crop heterogeneity on species traits of carabid beetles, spiders, butterflies and hoverflies and then tested the consequences of carabid beetle traits on biological control. In addition, we tested whether within-species trait variation was influenced by landscape crop heterogeneity, since the fitness of some carabid beetle species depend on landscape heterogeneity (Östman *et al.* 2001).

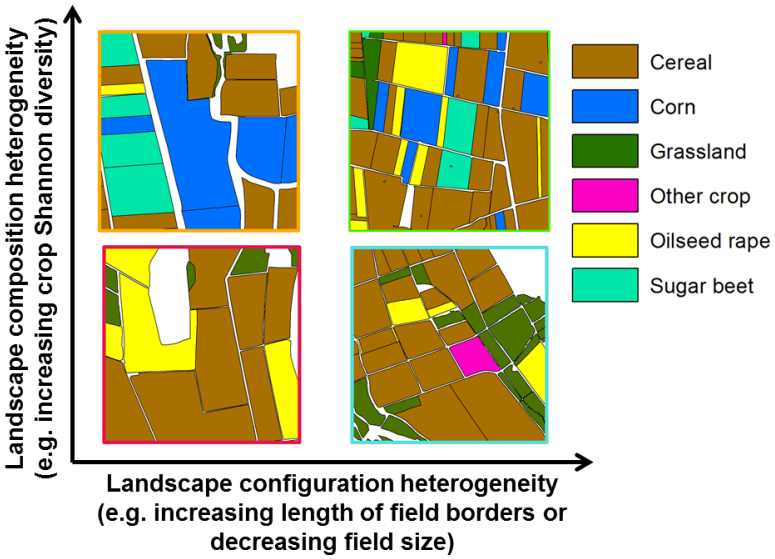


Fig. I1. Illustration of the two components of landscape heterogeneity focused on the cultivated area with an example of four landscapes (large squares, 1×1 km) found in the region around Göttingen in central Germany. The compositional heterogeneity increases with the diversity of crops types (number and/ or evenness of area proportion) and the configurational heterogeneity increases with the spatial complexity, i.e. increase in the length of field borders translating into decreased average field size.

Methods

The FarmLand project framework

The research presented in this thesis was carried out within the framework of the Biodiversa funded pan-European and Canadian project called FarmLand (http://farmland-biodiversity.org). FarmLand is a four year project involving research institutes of five countries: Carlton University (Canada), INRA, CNRS and Tour du Valat (France), University of Göttingen (Germany), British Trust for Ornithology (U.K.) and CTF Catalonia (Spain). This research consortium collaborated to disentangle the effect of landscape-wide crop compositional and crop configurational heterogeneity on biodiversity and ecosystem services. Common protocols for the study design and the biodiversity surveys were used to obtain comparable datasets along a wide range of agricultural regions. This thesis shows results from all eight study regions in chapter 1 (Europe and Canada Fig. B1 in Box 1), results from seven study regions in chapter 2 & 3 (Europe) and results from the Göttingen region in chapter 4 & 5.

Landscape selection

Within the eight studied regions (Fig. B1), we selected several 1 km x 1 km landscapes with on average 81% of cultivated land use along orthogonal gradients of crop compositional and configurational heterogeneity (Fig. I1). Landscape with high shares of cultivated area cover were chosen to maximize the length of the gradients of interest. The Shannon diversity metric was used as compositional heterogeneity gradient and field border length (or crop border length, see chapter 1) was used as configurational heterogeneity gradient. The Shannon diversity index was calculated across all crop types present in the landscapes, but considering all cereals as one crop type. Field edge length was calculated as the sum of field border length of all fields contained in one landscape. Hence, low values of field border length implied on average large field sizes in the landscape and high values implied small field sizes in the landscape. As metrics of crop diversity and field border length are naturally correlated in agricultural landscapes, we applied a specific landscape selection process described in Pasher *et al.* (2013) to ensure independence of both metrics. We first used a moving window approach, which screened all potential 1×1 km candidate landscapes (> 60% cultivated area) available in the region. Candidates were characterized by their crop diversity and field border length (Fig. 1a). These landscapes were then subdivided into four groups representing high and low values of heterogeneity gradients (Fig. 1a). From these groups, we selected between 32 and 92 landscapes per region distributed over 2 consecutive years (Fig.1b). We also ensured that landscapes were well distributed over the regions to avoid spatial autocorrelations with heterogeneity gradients.

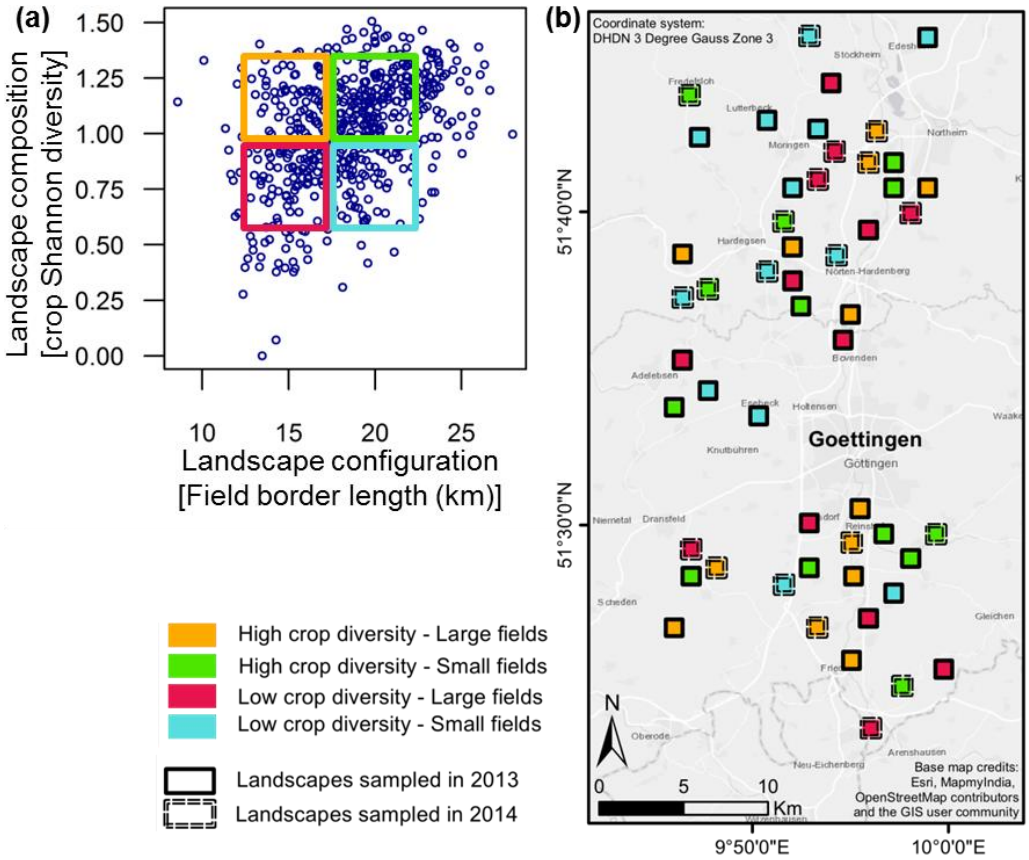


Fig. 1. Landscape selection process in the region of Göttingen. Illustration of the landscape crop composition and configuration of 559 landscape candidates (1×1 km) screened by the moving window method (a). From the four subsets of landscapes (a), a total of 52 landscapes randomly distributed over the region were selected for biodiversity sampling (b): 32 landscapes in 2013 and 20 landscapes in 2014.

Biodiversity sampling design

Within each landscape, we selected 4 fields of common crops cultivated in the regions. We sampled seven taxa (carabid beetles, spiders, bees, hoverflies, butterflies, birds and plants) in 3 of these fields (see details in chapter 1). Arthropods were surveyed twice in the growing season along 50m long transects, one at the field border and the other one 25m inside the field. Carabid beetles and spiders were sampled using pitfall traps (Fig. 2b & c), bees and hoverflies using pan traps and butterflies using sweep nets. Birds were surveyed by point count at the field border of all 4 sampling locations. Non-cultivated plants were recorded as ground-cover occupied by species along both transects (see details in chapter 1).

Collection and measurement of arthropod species traits

For carabid beetles, spiders, butterflies and hoverflies, we selected several species traits which are expected to be affected by landscape change (Tscharntke *et al.* 2012a) or related to ecosystem services of pest control and pollination (Schmitz 2007; Straub, Finke & Snyder 2008; Woodcock *et al.* 2014): species body size, foraging range, dispersal capacity and reproduction (see chapter 2). These traits were compiled for species collected in cereal fields of the European regions using available online databases and literature. Carabid beetles, spider and hoverflies species traits were collected mainly from three databases: the BETSI (Hedde *et al.* 2012), the carabids.org (Homburg *et al.* 2014) and the Syrph The Net (Speight *et al.* 2015) databases. Gaps in the databases were completed by further literature and expert knowledge. Butterfly traits were compiled from Bink (1992).

In addition, we measured the body condition and body length of individuals of three carabid beetle species: *Pterostichus melanarius* (Illiger 1798), *Poecilus cupreus* (Linné 1758) and *Anchomenus dorsalis* (Pontoppidan 1763). These species were abundant in cereal and oilseed rape fields in the region of Göttingen. Body condition trait in animals can be an indicator of health and potential reproductive success of individuals (Bommarco 1998; Knapp &

Knappová 2013). While landscape changes can affect arthropod assemblages based on species-level traits (e.g. Tscharntke *et al.* 2012), it can also affect traits within species, at the individual level (Bommarco 1998; Östman *et al.* 2001). Among sampled beetles in the region of Göttingen in 2013, we selected randomly from cereal and oilseed rape fields 3 females and 3 males of each species (between 187 and 379 specimens per species in total). We measured body condition (dry weight) and body length (elytra and pronotum length) of all individuals. Dry weight and body length are naturally dependent on each other. Body condition should reflect the status of a beetle independently from its size, thus we analysed body condition taking body length as a co-variable (Knapp & Knappová 2013)

Biological pest control potential estimation

In addition, we estimated biological pest control potential at the same period arthropods were collected in the fields. We measured aphid predation rates using aphids pasted on labels (Geiger *et al.* 2010; Bertrand, Baudry & Burel 2016). We placed 10 aphid labels per field (Fig. 2b & d). Three adult pea aphids *Acyrthosiphon pisum* were pasted on a 5×6 cm piece of sandpaper and frozen before introducing them into the field (Fig. 2e). The labels were fold like a tent to protect aphids from the rain and pinned to the ground, to allow easy access by ground-dwelling arthropods (Fig. 2d). After 24 hours of exposition in the fields, we recorded the number of aphids removed by predators. An aphid was considered as removed (i.e. predated) if we could recognised body leftovers on the aphid label (Fig. 2f).

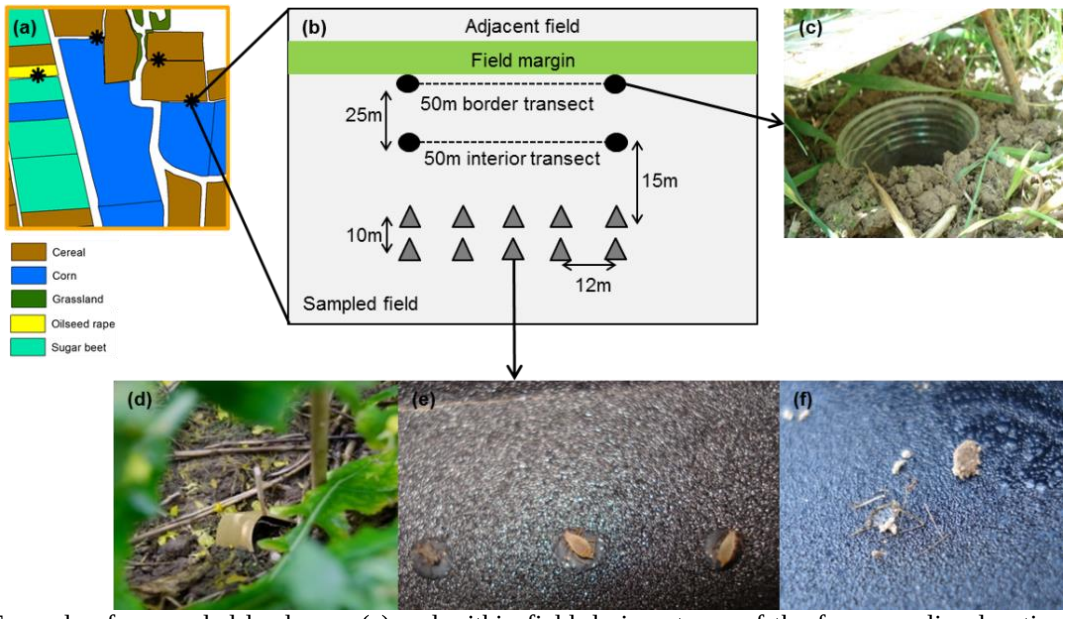


Fig. 2. Example of a sampled landscape (a) and within field design at one of the four sampling locations (b) for sampling carabid beetles and spiders with pitfall traps (c) and for estimating the biological control potential using aphid labels. Aphid labels were pinned at the soil surface like a tent protecting aphids from rain (d). We pasted three adult aphids per label (e). Aphids were considered as predated when remaining body parts were found on the label after 24 hours exposure in the field (f). *Photos by Jean-Louis Martin (d) and Aliette Bosem Baillod (c, e, f)*

Box 1. Description of the regions studied in the FarmLand project

The eight study regions are intensively cultivated areas in Canada, France, Germany, Spain and the United Kingdom (U.K.) (Fig. B1).

The Canadian region of Ontario is situated in the south of Ottawa and has a semi-continental climate. The region is dominated by corn, soybean and grassland and is interspersed with forest patches.

In France, four regions were studied. Armorique and PVDS (Plaine et Val de Sèvre) have both maritime climate. Armorique is dominated by grassland cereal and maize and is characterized by a hedgerow network surrounding most of the cultivated fields. PVDS is characterized by intensive farming of cereal, maize and sunflower. Coteaux is a region with continental, maritime and Mediterranean climate influence. This hilly region is dominated by cereal, grassland and sunflower crops. The Camargue region is contrasting with its Mediterranean climate, located in the Rhône river delta. This coastal agricultural region is characterized by floods and high soil salinity. In these conditions, agricultural landscapes are primarily devoted to intensive rice cultivation alternating with cereals.

In the centre of Germany, the hilly region of Göttingen is influenced by both continental and maritime climate. The region is dominated by cereals, oilseed rape, maize, grassland and sugar beet crops. Most of the grasslands are intensively managed. This region is interspersed by forest patches and semi-natural calcareous grasslands.

The pseudo-steppe region of Lleida in Spain has a Mediterranean climate. The studied region is dry, but crops are not intensively irrigated. The region is dominated by cereals, almond and olive plantations. The area is interspersed with shrubland and oak forest patches.

Finally, the region of East-Anglia in the U.K. with maritime climate is dominated by arable crops such as cereals and oilseed rape as well as grasslands.

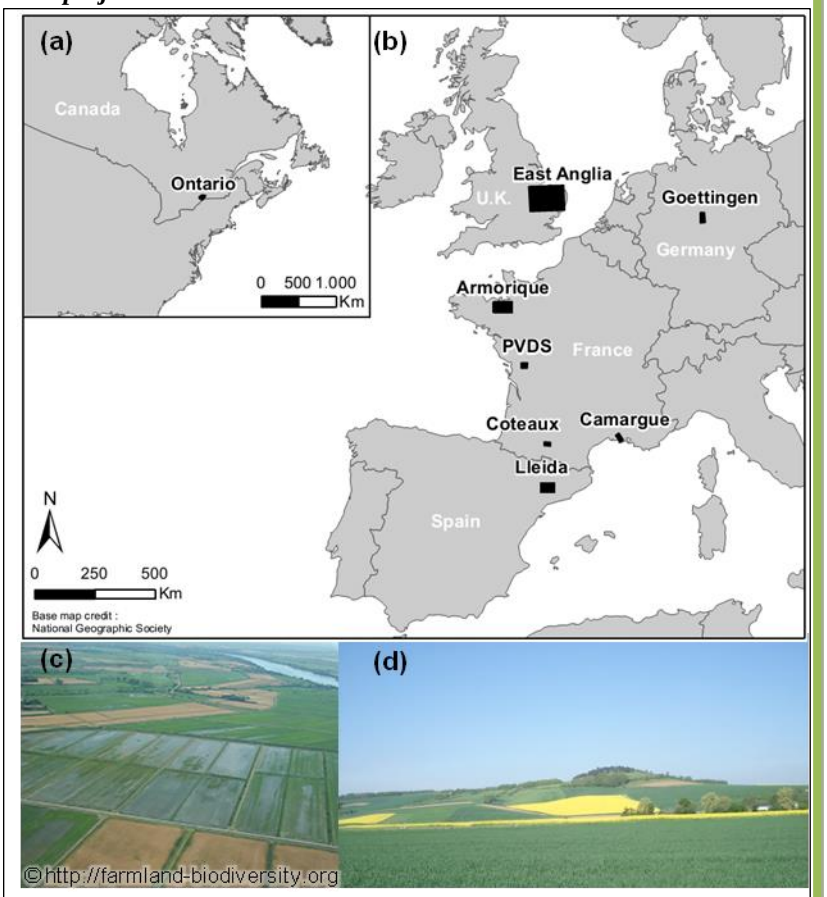


Figure B1. Location of the study regions within a north-American country (a) and four European countries (b). Illustration of two contrasting regions: the rice dominated Camargue region (c) and the cereal dominated Göttingen region (d).
Photo by Aliette Bosem Baillod (d)

Research objectives

In this thesis, I study the effect of landscape-wide crop heterogeneity on species taxonomic and functional diversity, pests and the ecosystem service of biological pest control. The aim was to disentangle spatial composition and configuration effects as well as temporal composition effects on biodiversity and ecosystem service. Following questions were answered:

(1) Does the compositional and configurational heterogeneity of crops in the landscape enhance species diversity of animals and plants?

(2) How does the compositional and configurational heterogeneity of crops affect species traits of arthropods?

(3) Are the functional diversity and community level traits of ground-dwelling arthropods affected by landscape-wide crop heterogeneity? Is the effect of landscape-wide crop heterogeneity on biological control potential mediated by community functional diversity?

(4) Do aphid pest, their enemies and biological control depend on landscape-wide composition and configuration of crops in space and time?

Chapter outline

Chapter 1 is focused on the first question using biodiversity data of seven taxa (carabid beetle, spider, hoverfly, butterfly, bee, bird and plant) collected in Europe and North-America. The chapter disentangle the effect of crop composition (crop Shannon diversity) and crop configuration (length of field borders) on the taxonomic diversity of animal and plants. To achieve this goal, biodiversity was surveyed in crop habitats which surrounding landscape followed independent gradients of crop composition and configuration

Chapter 2 addresses the second question. This chapter presents a follow-up study of the first chapter, giving more insights of landscape effects on species. Information about life-history traits relevant for biological control and pollination services was collected for species of carabid beetles, spiders, butterflies and hoverflies. Traits included in the study were body size, dispersal, foraging and reproduction strategies of species. Using a multi-dimensional ordination method RLQ, we showed how components of landscape-wide crop heterogeneity and semi-natural habitat cover filtered species traits.

Chapter 3 focuses on the third question. Here I investigated the effect of (1) landscape-wide crop heterogeneity and semi-natural habitats on the functional diversity and the dominant traits within communities of carabid beetle and spiders and (2) the cascading effect of landscape and carabid beetle community's traits on biological pest control potential. Community's dominant traits were defined as community weighted mean for each trait. Hence it is a measure characterising a community by its mean value for one trait, weighted by the abundance of species in the community. The functional diversity was defined by functional dispersion which is a measure of trait variability or complementarity at the community level (Laliberté & Legendre 2010). I used structural equation model to assess the direct and indirect effects of landscape variables on community traits and biological control potential using the data collected in the seven European regions.

Chapter 4 adresses the fourth question. With a focus on pests and associated arthropods I show that the effect of landscape depends on the spatial and temporal heterogeneity of crops. We surveyed aphids, their vegetation-dwelling enemies and parasitized aphids in cereal fields around Göttingen. Landscapes around cereal fields were selected along gradients of crop diversity, field border and grassy boundary length (spatial landscape heterogeneity) and inter-annual change in resource habitats for aphids (temporal landscape heterogeneity). We showed that aphids, parasitism and enemies respond to complex interactions between spatial and temporal crop heterogeneity in landscapes.

Chapter 5 gives further insights on the second and third question. This chapter presents preliminary results and is at an early stage of preparation. I present in this chapter results from the region of Göttingen on the relation between landscape-wide crop diversity, field border density and semi-natural habitat on carabid beetle body size and body condition. In this chapter I compared the effect of landscape on inter-specific (at the community level) and intra-specific traits (within three species). To achieve this goal, we collected the mean body size of all sampled beetles from the literature and measured the length of the body and the dry weight of three common species caught in cereal and oilseed rape fields: *Anchomenus dorsalis* (Pontoppidan 1763), *Poecilus cupreus* (Linné 1758) and *Pterostichus melanarius* (Illiger 1798).

Conclusions

The results of the five studies showed that compositional and configurational heterogeneities of crops in agricultural landscape influence the diversity of multiple taxa, pest abundance, species traits and the biological control of pests.

The first study on multiple taxa, demonstrated that the reduction in average field size benefited the diversity of most arthropods and an increase in crop diversity enhanced bird and plant diversity. The second study gave additional insights by showing that arthropod communities with specialised traits (low reproductive rates or specialised feeding habits) were favoured in landscapes with small fields (butterflies and carabid beetles) or in landscapes with higher diversity of crops (hoverflies). These studies showed that not only species numbers can benefit from crop heterogeneity, but specialized species as well, which are usually declining in homogenous and intensified landscapes (Gámez-Virués *et al.* 2015). The third study integrated these findings to test the consequences on the ecosystem service of biological pest control. We showed that the landscape-scale crop diversity had a hump-shaped effect on biological pest control, but this effect was not mediated by carabid-beetle traits. However, biological control was enhanced when carabid beetle communities were dominated by omnivorous species. These findings demonstrate that landscape and trait driven effect on biological control may operate separately. The hump-shaped effect of landscape-wide crop diversity on biological control suggests that crop diversity may be beneficial to a tipping point, until adding more of certain intensively managed crops reverse the effect. The fourth study concentrate on the spatial and temporal crop heterogeneity on aphid pests. The most important findings were that (1) higher crop diversity in the landscape could decrease aphid abundance only when aphid-host crops were reduced compared to the previous year and (2) reducing field sizes while keeping high amounts of grassy field boundaries in the landscape could also reduce aphid abundance. This emphasized the importance of crop rotations and suggest that small-field landscapes with alternating host-crop and non-host crop resources may reduce pest pressure. Further, the last study focused on carabid beetle inter and intra-species body size and body condition variation. We found that higher crop diversity in the landscape would favour larger species which are more sensitive to management practices. Contrastingly, small-field landscapes may favour small species which often depend on dispersion from semi-natural habitats into crops. In addition, larger body size within the species *P. cupreus* suggested better feeding conditions in small-field landscapes.

Overall, we conclude that maintaining and promoting landscape crop heterogeneity through higher crop diversity and reduction in mean field size may benefit diversity of multiple taxa and sustain specialized species. However, interference with other than spatial factors may constrain the consequences on pest pressure and biological control. Pest pressure likely depends on the succession of host and non-host crops in the landscape, emphasising the importance of alternating these crop types in crop rotations. Biological control can be enhanced when crop diversification is not accompanied with management intensification. Currently, the common agricultural policies in Europe face heavy criticism because the greening measures cannot halt biodiversity declines (Pe'er *et al.* 2014). Most of the greening measures are agri-environmental schemes promoting more semi-natural habitats or less disturbed areas (e.g. flower strips, fallow, grasslands). The positive effects of landscape-wide crop diversity and reduced field size on biodiversity and biological control found in our studies, may give a new perspective on biodiversity conservation. In the future, crop patterns could be integrated in the design of policies aiming to conserve biodiversity, although more research is needed to test whether crop heterogeneity can add up with other greening measures to promote biodiversity in agricultural landscapes.

References

Altieri, M.A. (1999) The ecological role of biodiversity in agroecosystems. *Agriculture, Ecosystems & Environment*, **74**, 19–31.

Benton, T.G., Vickery, J.A. & Wilson, J.D. (2003) Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology & Evolution*, **18**, 182–188.

Bertrand, C., Baudry, J. & Burel, F. (2016) Seasonal variation in the effect of landscape structure on ground-dwelling arthropods and biological control potential. *Basic and Applied Ecology*.

Bertrand, C., Burel, F. & Baudry, J. (2016) Spatial and temporal heterogeneity of the crop mosaic influences carabid beetles in agricultural landscapes. *Landscape Ecology*, **31**, 451–466.

Bianchi, F.J.J.A., Booij, C.J.H. & Tscharntke, T. (2006) Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. *Proceedings of the Royal Society of London B: Biological Sciences*, **273**, 1715–1727.

Bink, F.A. (1992) *Ecologische atlas van de dagvlinders van Noordwest-Europa*. Schuyt & Co Uitgevers en Importeurs, Haarlem.

Bommarco, R. (1998) Reproduction and Energy Reserves of a Predatory Carabid Beetle Relative to Agroecosystem Complexity. *Ecological Applications*, **8**, 846–853.

Chaplin-Kramer, R., O'Rourke, M.E., Blitzer, E.J. & Kremen, C. (2011) A meta-analysis of crop pest and natural enemy response to landscape complexity. *Ecology Letters*, **14**, 922–932.

Dunning, J.B., Danielson, B.J. & Pulliam, R.H. (1992) Ecological processes that affect populations in complex landscapes. *Oikos*, **65**.

Fahrig, L., Baudry, J., Brotons, L., Burel, F.G., Crist, T.O., Fuller, R.J., Sirami, C., Siriwardena, G.M. & Martin, J.-L. (2011) Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecology letters*, **14**, 101–112.

Firbank, L.G., Petit, S., Smart, S., Blain, A. & Fuller, R.J. (2008) Assessing the impacts of agricultural intensification on biodiversity: a British perspective. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, **363**, 777–787.

Gámez-Virués, S., Perović, D.J., Gossner, M.M., Börschig, C., Blüthgen, N., de Jong, H., Simons, N.K., Klein, A.-M., Krauss, J., Maier, G., Scherber, C., Steckel, J., Rothenwöhrer, C., Steffan-Dewenter, I., Weiner, C.N., Weisser, W., Werner, M., Tscharntke, T. & Westphal, C. (2015) Landscape simplification filters species traits and drives biotic homogenization. *Nature Communications*, **6**, 8568.

Geiger, F., Bengtsson, J., Berendse, F., Weisser, W.W., Emmerson, M., Morales, M.B., Ceryngier, P., Liira, J., Tscharntke, T., Winqvist, C., Eggers, S., Bommarco, R., Pärt, T., Bretagnolle, V., Plantegenest, M., Clement, L.W., Dennis, C., Palmer, C., Oñate, J.J., Guerrero, I., Hawro, V., Aavik, T., Thies, C., Flohre, A., Hänke, S., Fischer, C., Goedhart, P.W. & Inchausti, P. (2010) Persistent negative effects of pesticides on biodiversity and biological control potential on European farmland. *Basic and Applied Ecology*, **11**, 97–105.

Hedde, M., Pey, B., Auclerc, A., Capowiez, Y., Cluzeau, D., Cortet, J., Decaëns, T., Deharveng, L., Dubs, F., Joimel, S., Guernion, M., Grumiaux, F., Laporte, M.-A., Nahmani, J., Pasquet, A., Pelosi, C., Pernin, C., Ponge, J.-F., Salmon, S. & Santorufo, L. (2012) BETSI, a complete framework for studying soil invertebrate functional traits. Coimbra.

Holland, J.M. (2002) *The Agroecology of Carabid Beetles*. Intercept, Andover.

Homburg, K., Homburg, N., Schäfer, F., Schuldt, A. & Assmann, T. (2014) Carabids.org - a dynamic online database of ground beetle species traits (Coleoptera, Carabidae) eds C. Dytham & R. Ewers. *Insect Conservation and Diversity*, **7**, 195–205.

Knapp, M. & Knappová, J. (2013) Measurement of Body Condition in a Common Carabid Beetle, *Poecilus cupreus* : A comparison of Fresh Weight, Dry Weight, and Fat Content. *Journal of Insect Science*, **13**, 1–10.

Laliberté, E. & Legendre, P. (2010) A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, **91**, 299–305.

Östman, Ö., Ekbom, B., Bengtsson, J., Weibull, A.-C. & Ostman, O. (2001) Landscape Complexity and Farming Practice Influence the Condition of Polyphagous Carabid Beetles. *Ecological Applications*, **11**, 480.

Palmu, E., Ekroos, J., Hanson, H.I., Smith, H.G. & Hedlund, K. (2014) Landscape-scale crop diversity interacts with local management to determine ground beetle diversity. *Basic and Applied Ecology*, **15**, 241–249.

Pasher, J., Mitchell, S., King, D., Fahrig, L., Smith, A. & Lindsay, K. (2013) Optimizing landscape selection for estimating relative effects of landscape variables on ecological responses. *Landscape Ecology*, **28**, 371–383.

Pe'er, G., Dicks, L.V., Visconti, P., Arlettaz, R., Báldi, A., Benton, T.G., Collins, S., Dieterich, M., Gregory, R.D., Hartig, F., Henle, K., Hobson, P.R., Kleijn, D., Neumann, R.K., Robijns, T., Schmidt, J., Shwartz, A., Sutherland, W.J., Turbé, A., Wulf, F. & Scott, A.V. (2014) EU agricultural reform fails on biodiversity. *Science*, **344**, 1090–1092.

Rusch, A., Birkhofer, K., Bommarco, R., Smith, H.G. & Ekbom, B. (2015) Predator body sizes and habitat preferences predict predation rates in an agroecosystem. *Basic and Applied Ecology*, **16**, 250–259.

Schmitz, O.J. (2007) Predator diversity and trophic interactions. *Ecology*, **88**, 2415–2426.

Speight, M.C.D., Castella, E., Sarthou, J.-P. & Vanappelghem, C. (2015) *Syrph the Net: The Database of European Syrphidae*, Syrph the Net publications. Dublin.

Stoate, C., Báldi, A., Beja, P., Boatman, N.D., Herzon, I., van Doorn, A., de Snoo, G.R., Rakosy, L. & Ramwell, C. (2009) Ecological impacts of early 21st century agricultural change in Europe – A review. *Journal of Environmental Management*, **91**, 22–46.

Straub, C.S., Finke, D.L. & Snyder, W.E. (2008) Are the conservation of natural enemy biodiversity and biological control compatible goals? *Biological Control*, **45**, 225–237.

Thies, C., Steffan-Dewenter, I. & Tscharntke, T. (2008) Interannual landscape changes influence plant–herbivore–parasitoid interactions. *Agriculture, Ecosystems & Environment*, **125**, 266–268.

Tscharntke, T., Bommarco, R., Clough, Y., Crist, T.O., Kleijn, D., Rand, T.A., Tylianakis, J.M., Nouhuys, S. van & Vidal, S. (2007) Conservation biological control and enemy diversity on a landscape scale. *Biological Control*, **43**, 294–309.

Tscharntke, T., Tylianakis, J.M., Rand, T.A., Didham, R.K., Fahrig, L., Batáry, P., Bengtsson, J., Clough, Y., Crist, T.O., Dormann, C.F., Ewers, R.M., Fründ, J., Holt, R.D., Holzschuh, A., Klein, A.M., Kleijn, D., Kremen, C., Landis, D.A., Laurance, W., Lindenmayer, D., Scherber, C., Sodhi, N., Steffan-Dewenter, I., Thies, C., van der Putten, W.H. & Westphal, C. (2012) Landscape moderation of biodiversity patterns and processes - eight hypotheses. *Biological Reviews*, **87**, 661–685.

Westphal, C., Steffan-Dewenter, I. & Tscharntke, T. (2009) Mass flowering oilseed rape improves early colony growth but not sexual reproduction of bumblebees. *Journal of Applied Ecology*, **46**, 187–193.

Woodcock, B.A., Harrower, C., Redhead, J., Edwards, M., Vanbergen, A.J., Heard, M.S., Roy, D.B. & Pywell, R.F. (2014) National patterns of functional diversity and redundancy in predatory ground beetles and bees associated with key UK arable crops. *Journal of Applied Ecology*, **51**, 142–151.

CHAPTER 1
Enhancing biodiversity across taxa and regions by increasing multiple components of agricultural landscape heterogeneity

Article in preparation

Clélia Sirami, **Aliette Bosem Baillod***, Colette Bertrand*, Romain Carrié*, Annika Hass*, Laura Henckel*, Paul Miguet*, Carole Vuillot*, Audrey Alignier, Jude Girard, Péter Batáry, Yann Clough, Cyrille Violle, David Giralt, Gerard Bota, Isabelle Badenhauser, Gaetan Lefebvre, Nicolas Gross, Bertrand Gauffre, Aude Vialatte, François Calatayud, Assu Gil-Tena, Nora Quesada-Pizarro, Lutz Tischendorf, Scott Mitchell, Kathryn Lindsay, Romain Georges, Samuel Hilaire, Jordi Recasens, Jordi Bosch, Jose Antonio Barrientos, Antonio Ricarte, Mª Ángeles Marcos, Jesus Minano, Raphael Mathevet, Annick Gibon, Jacques Baudry, Gerard Balent, Brigitte Poulin, Françoise Burel, Teja Tscharntke, Vincent Bretagnolle, Gavin Siriwardena, Annie Ouin, Lluis Brotons, Jean-Louis Martin**, Lenore Fahrig**

*These co-authors contributed equally as part of their PhDs and should be considered co-second authors.
**These co-authors contributed equally to the project coordination and should be considered co-last authors.

Abstract

Studies on the effect of landscape heterogeneity on biodiversity in agricultural landscapes have predominantly focused on the amount of semi-natural habitats while ignoring the role of the crop mosaic. In the current context of repeated criticisms towards current agricultural policies, it is however crucial to know whether managing the crop mosaic could benefit biodiversity. We investigated the effect of cropland compositional and configurational heterogeneity on species richness across seven taxa and 435 landscapes located in eight regions of Europe and North America. We show for the first time that increasing cropland compositional and configurational heterogeneity can have a positive effect on biodiversity across taxa, independently from the effects of the amount of semi-natural habitat and the length of semi-natural boundaries. These effects are consistent across ecoregions, countries and landscape types. Both cropland compositional and configuration heterogeneity had a significant effect on biodiversity, each component of cropland heterogeneity influencing different sets of taxa. Our study therefore shows that managing the crop mosaic while maintaining the amount and spatial distribution of semi-natural habitats would benefit biodiversity both across taxa and regions.

Introduction

The role of landscape heterogeneity on biodiversity is a central theme in landscape ecology (Dunning, Danielson & Pulliam 1992). Landscape heterogeneity has been shown to positively influence species richness of various taxa in a wide-range of systems (Stein, Gerstner & Kreft 2014), although negative, unimodal and non-significant heterogeneity-diversity relationships have been frequently reported as well (e.g. Bar-Masada & Wood 2014). Several mechanisms have been proposed to explain these relationships, including increasing niche diversity, higher potential for resource complementation (Dunning, Danielson & Pulliam 1992; Andren, Delin & Seiler 1997), stabilization of species interactions (Danielson 1991) as well as negative edge effect, minimum patch size requirements and area-heterogeneity trade-offs (Allouche 2012). Landscape heterogeneity can influence species richness through compositional and configurational heterogeneity (See box 1 for detailed hypotheses; Fahrig *et al.* 2011).

There has been a recent explosion of research on the effects of landscape heterogeneity on biodiversity in agricultural landscapes. This research is rooted in the increasing awareness that farming systems dominate the world's terrestrial area (Tilman *et al.* 2001; Foley *et al.* 2005) and that impacts on biodiversity in these systems are critical for future biodiversity conservation and the delivery of multiple ecosystems services to human populations (Krebs *et al.* 1999; Donald, Green & Heath 2001; Gregory, G. Noble & Custance 2004; Tscharntke *et al.* 2005; Butler, Vickery & Norris 2007; Robertson *et al.* 2014). Studies in agricultural landscapes have shown that landscape heterogeneity positively influences species richness of various taxa (Benton, Vickery & Wilson 2003; Miyashita, Chishiki & Takagi 2012; Perović *et al.* 2015 but see Hawro *et al.* 2015). However, a majority of these studies has used the amount of semi-natural habitat as a proxy for farmland heterogeneity (e.g. Roschewitz *et al.* 2005; Holzschuh, Steffan-Dewenter & Tscharntke 2010; Poggio, Chaneton & Ghersa 2010; Winqvist, Ahnström & Bengtsson 2012), based on the assumption that these are the main reservoirs of biodiversity within agricultural landscapes.

While it may be true that a large proportion of biodiversity occurs in the semi-natural habitats of agricultural landscapes, there is nevertheless a wide gradient in resources offered in different cover types within cropped habitats (Henderson, Vickery & Carter 2004; Holzschuh *et al.* 2013; Raymond *et al.* 2014). The increasing demand for agricultural products has driven the conversion of natural habitat into agricultural land but has also resulted in simplified crop patterns with larger fields and fewer crop types. As availability of semi-natural habitat in agricultural landscape is low and maintaining or restoring these habitats is politically controversial (Burton, Kuczera & Schwarz 2008), it is of increasing interest to know whether enhancing farmland heterogeneity simply by modifying the configuration and composition of the crop mosaic may also have a beneficial effect on biodiversity (See box 2).

We tested this idea by conducting a multi-region, multi-taxa study using a common methodology. We defined farmland heterogeneity in terms of two independent axes representing farmland compositional heterogeneity and farmland configurational heterogeneity (Figure 1). We selected eight agricultural regions to increase the farmland heterogeneity gradient and to test whether heterogeneity-biodiversity relationships hold across different ecoregions and agricultural systems. We selected seven taxa to test whether heterogeneity-biodiversity relationships hold across different taxa. We addressed the following questions: (i) what are the relative effects of farmland compositional heterogeneity, farmland configurational heterogeneity and the amount of semi-natural habitat on biodiversity? (ii) are these effects independents from each other? (iii) are these effect non-linear? and (iv) are these effects consistent across regions?

Methods

1. Region and landscape selection

We selected eight agricultural regions (Figure 2), aiming to increase the landscape heterogeneity gradient and to test whether heterogeneity-biodiversity relationships hold across different ecoregions and agricultural systems. These eight agricultural regions belonged to six different ecoregions (as defined in Olson *et al.* 2001), presented some variations in terms of topography, climate, complexity in crop field shapes, diversity of crop types or agricultural products. Regions were also selected on the basis of local availability of researchers with expertise in landscape analysis and sampling and identification of a wide range of taxa.

Within each agricultural region, we selected several 1 km x 1 km agricultural landscapes (i.e. 60-90% of crop cover), within which we sampled seven taxa (below). Between 32 and 93 landscapes were sampled per region, totalling 435 landscapes, with an average of 81±9.8% of crop cover across the eight regions. Landscapes in each region were selected based on cropland compositional heterogeneity and configurational heterogeneity using the best spatial data available (detailed methods in Pasher *et al.* 2013). We used Shannon diversity of crops as our index of compositional heterogeneity and total length of crop field boundaries as our index of configurational heterogeneity. Within each region, landscapes were selected to maximise the compositional and configurational heterogeneity gradients while reducing correlation between gradients, as well as between cropland heterogeneity and geographical gradients. Additional details on region and landscape selection are provided in Appendix 1 and 4.

2. Biodiversity sampling

Plants, bees, butterflies, syrphids, carabids, spiders and birds were sampled as biodiversity proxies in all landscapes. These taxa were selected because they are (i) easy to sample across a large number of sites, and (ii) represent a wide range of ecological functions, including multiple trophic levels and mediation of several ecosystem services in agricultural systems.

Biodiversity sampling took place from 2011 to 2014 using identical sampling protocols across all regions, thus allowing us to estimate overall effects of landscape heterogeneity on biodiversity and to compare consistency of effects across the eight regions. Each landscape was sampled in one year only. Within each of the 435 1 km x 1 km landscapes, we selected three fields as sampling sites. Sampling was carried out along two parallel 50 m 'transects', one located at the field edge, the other 25 m away inside the field (Figure A in Appendix 2). The three sampling sites were at least 200 m apart, at least 50 m from the border of the 1 km x 1 km landscape, and at least 50 m from patches of semi-natural habitats such as forests. Within these constraints, we tried to select sampling sites based on the dominant crop types within each region. For example, in Goettingen, we sampled two wheat fields and one oilseed rape field in each landscape. When this was not feasible, we selected sampling sites based on crop types available within a given landscape, trying to avoid correlation between crop type sampled and the two cropland heterogeneity gradients as much as possible.

At each site, birds were sampled using point-counts centred on the field-edge transect. Plants were surveyed in a series of quadrats along both transects. Butterflies were surveyed by visual cues using timed-walks along both transects. Bees and syrphids were sampled using coloured pan traps on poles erected at each end and in the centre of both transects. Carabids and spiders were sampled using pitfall traps installed at each end of both transects. Captured insects were preserved in ethanol for further identification. Altogether sampling occurred at 2610 transects, at 1305 sample sites within 435 landscapes and we identified more than 167,028 individuals from 2795 species. Details of the sampling site selection and biodiversity sampling methods can be found in Appendix 2.

3. Cropland compositional and configurational heterogeneity

As described above, landscape selection within each region was based on the best spatial data available in each region before initiation of field work. However, in order to maximize the accuracy of the heterogeneity metrics and homogenize the methods for calculating landscape metrics among regions, we conducted extensive ground-truthing to produce high-resolution land cover maps simultaneously to field work. All crop fields, boundaries between two crop fields and non-agricultural habitat patches were mapped. We built a land cover classification common to all eight regions. Crop types included: cereal, fallow, alfalfa, clover, ryegrass, grassland, rice, corn, sunflower, sorghum, millet, moha, oilseed rape, mustard, pea, bean, soybean, linseed, orchard, almond, olive, vineyard, mixed vegetables, sugar beet, asparagus, carrot, onion, parsnip, potato, tomato, melon, strawberry, raspberry, wild bird cover. Non-crop habitats included: woodland, open land, wetland and built-area. We then re-calculated Shannon diversity of crop types and total crop border length for each landscape, based on these detailed maps and the common crop type classification. Figure 3 shows the range of values of cropland compositional and crop configurational heterogeneity in each region.

Because we already know that the amount of semi-natural habitat and its spatial distribution in the landscape have a major influence on biodiversity, we calculated two other landscape variables. We calculated the percentage of semi-natural habitat (i.e. woodland, open land, wetland including narrow linear habitats) within each landscape, as well as the amount of linear semi-natural habitats between fields (e.g. the total length of hedgerows, grassy strips, tracks, ditches) within each landscape. Details of the landscape mapping and landscape variable calculation can be found in Appendix 3.

4. Effects of cropland compositional and configurational heterogeneity

We tested the effects of cropland compositional and cropland configurational heterogeneity on biodiversity using mean alpha diversity for each taxon as a response variable, the landscape variables of interest (i.e. Shannon diversity of crop types and total crop border length) as well as the covariates (i.e. the percentage cover of semi-natural habitats and the total length of semi-natural boundaries) as explanatory variables. Our objectives when selecting the eight agricultural regions were 1) to test heterogeneity-biodiversity relationships on longer farmland heterogeneity gradients and 2) to test whether heterogeneity-biodiversity relationships hold across different ecoregions and agricultural systems. As a result, we tested the effects of cropland compositional and cropland configurational heterogeneity on biodiversity at two levels.

First, we tested the effects of cropland compositional and cropland configurational heterogeneity on biodiversity across regions, i.e. we considered that the eight regions represent one single gradient of cropland compositional and cropland configurational heterogeneity (Figure 4-1a). To do this, we used simple linear models with no region effect. To test whether the effects are independent or interacting, we compared this linear model with and without an interaction term between cropland compositional and cropland configurational heterogeneity (Figure 4-1b). To test whether the effects are linear or non-linear, we compared each one of these three models with and without quadratic terms for cropland compositional and cropland configurational heterogeneity (Figure 4-1c). We considered that our hypotheses (interacting or non-linear effects) were supported when ΔAIC (null model – model of interest) > 2.

Second, we tested the effect of cropland compositional and cropland configurational heterogeneity on biodiversity within regions, i.e. we considered that the eight regions are random replicates of the two cropland compositional and cropland configurational heterogeneity gradients (Figure 4-2a). To do this, we used linear mixed models with region as a random effect. Within this second level, we compared a linear mixed model with a random region effect on intercept only versus on intercept and slope to test whether the effects of cropland compositional and cropland configurational heterogeneity on biodiversity differ between regions (Figure 4-2b). We considered that our hypothesis (regional effect on slope) was supported when ΔAIC (model with random effect on intercept – model with random effect on intercept and slope) > 2.

All explanatory variables and covariates were standardized to allow a direct comparison of estimates. We ran diagnostic tools to verify that residuals were independently and normally distributed. All analyses were conducted in R 3.2.5. Appendix 4 provides more details about the statistical analyses as well as the mean and standard deviation of mean alpha diversity for each taxon as well as the correlations among explanatory variables.

Results

When considering a single gradient across all eight regions, we detected a significant effect of cropland heterogeneity on alpha diversity, independent of the effect of the amount of semi-natural habitats, for all seven taxa except bee (Figure 5-1). Cropland configurational heterogeneity had a significant effect on four taxa (butterfly, carabid, spider and syrphid) while cropland compositional heterogeneity had a significant effect on two taxa (bird and plant). All significant effects were positive, except the effect of cropland configurational heterogeneity on butterfly diversity. We detected a significant ad positive interacting effect between cropland compositional and cropland configurational heterogeneity for syrphid (Table 1). We also detected significant non-linear effects of cropland compositional and cropland configurational for butterfly, carabid, spider and syrphid (Table 1).

When considering replicated gradients within regions, we detected a significant effect of cropland heterogeneity on alpha diversity, independent of the effect of the amount of semi-natural habitats, on three of the seven taxa (Figure 5-2). Cropland configurational heterogeneity had a significant effect on bee while cropland compositional heterogeneity had a significant effect on bird and plant. All significant effects were positive. We detected a significant random effect of region on the slope only for butterfly (Table 1).

Box 1. General hypotheses linking biodiversity to landscape heterogeneity

1. Compositional Heterogeneity

Hyp 1a. Biodiversity **increases** with cover type diversity if cover types represent availability of different resources, so different cover types can support different species. In addition, different cover types may represent different required resources for a single species (landscape complementation). This is one of the main hypotheses tested in the literature on landscape heterogeneity.

Hyp 1b. Biodiversity **decreases** with cover type diversity if most species have high minimum total habitat area requirements. An increase in the number of cover types results in a decrease in total area of each cover type, so there are insufficient resources provided by some cover types to support all their species (Fahrig *et al.* 2011; Tscharntke *et al.* 2012). This is the main hypotheses tested in the literature on habitat loss.

Hyp 1c. Biodiversity shows a **peaked relationship** with cover type diversity (Allouche *et al.* 2012). Initially there is an increase in biodiversity with increasing cover type diversity for reasons explained in Hyp 1a, but at higher levels of cover type diversity, each cover type has a lower spatial cover and biodiversity decreases for reasons explained in Hyp 1b.

2. Configurational Heterogeneity

Hyp 2a. Biodiversity **increases** with increasing border length or decreasing mean patch size in the landscape if borders result in increased habitat connectivity for most species, if landscapes with larger patches have lower permeability for most species, and/or accessibility to multiple habitats for many species (landscape complementation) is increased. This is one of the main hypotheses tested in the literature on landscape heterogeneity.

Hyp 2b. Biodiversity **decreases** with increasing border length or decreasing mean patch size in the landscape if most species show negative edge effects, if most species have minimum patch size requirements (separate from their total habitat area requirements, see Hyp1b), and/or if larger patches have higher permeability for most species. This is one of the main hypotheses tested in the literature on habitat fragmentation.

Hyp 2c. Biodiversity shows a **peaked relationship** with increasing border length or decreasing mean patch size in the landscape. Initially there is an increase in biodiversity for reasons explained in Hyp 2a and when mean patch size reaches minimum patch size requirements for most species, biodiversity decreases.

Box 2. Traditional versus novel approaches to enhance biodiversity in agricultural landscapes: increasing landscape heterogeneity (i.e. semi-natural habitats) versus increasing farmland heterogeneity (i.e. modifying only the crop mosaic).

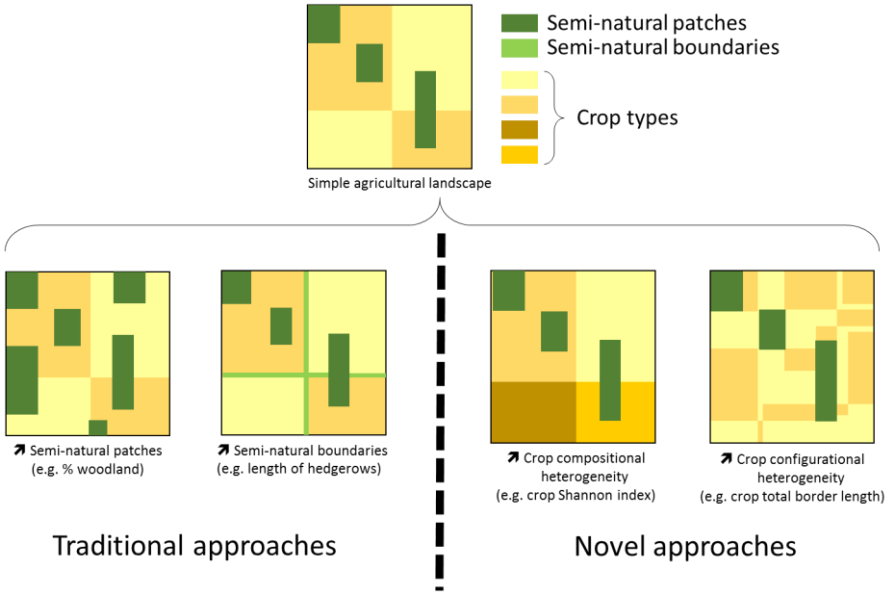


Table 1. Comparison of model AIC values for each taxon and each level of analysis: 1) single gradient across regions and 2) replicated gradients within regions. Values in bold correspond to models for which ΔAIC (null model 1a or 2a – model of interest) > 2.

	1. Single gradient across regions			2. Gradients within regions	
Taxon	1a. linear	1b. interacting	1c. non-linear	2a. intercept	2b. slope
bee	1013.94	1015.13	1013.12	939.771495	948.70347
bird	2000.79	1998.82	2000.64	1961.56496	1963.87288
butterfly	1584.30	1583.17	**1576.32**	1417.83641	**1410.21864**
carabid	2298.08	2296.70	**2268.71**	1972.19756	1975.19852
plant	3163.39	3165.05	3166.69	2941.88627	2948.4184
spider	2572.68	2574.64	**2549.66**	2282.55896	2289.26291
syrphid	1841.04	**1838.35**	**1829.13**	1759.64015	1766.79203

Figure 1. Illustration of the two major components of landscape spatial structure: compositional and configurational heterogeneity (from Fahrig *et al.* 2011). Each large square is a landscape and different colours represent different cover types within landscapes. Compositional heterogeneity increases with increasing number and/or evenness of cover types. Configurational heterogeneity increases with increasing complexity of the spatial pattern.

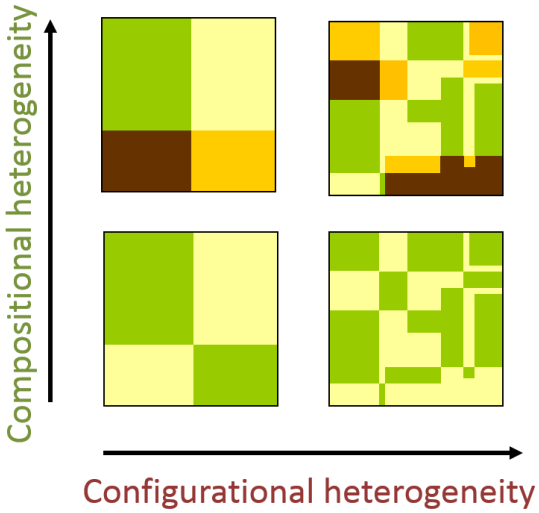


Figure 2. Location of the eight study regions in Europe and North America (top left insert) and illustration of the location of landscapes sampled in one of the eight regions, the Plaine et Val de Sèvre (PVDS) study area (bottom left insert).

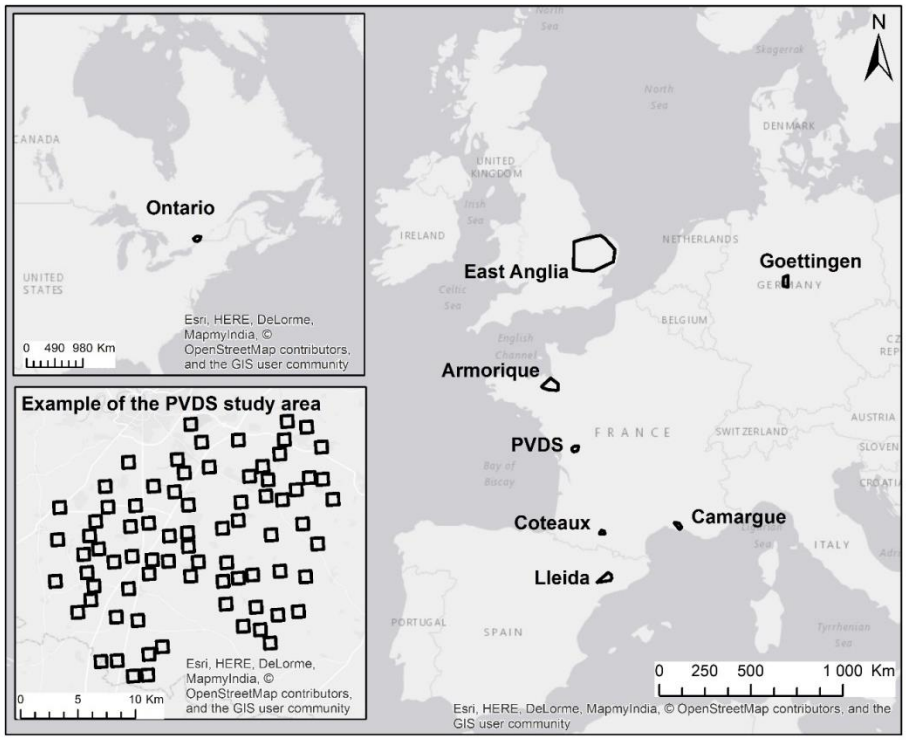


Figure 3. Variation in cropland compositional and configurational heterogeneity sampled across the eight regions. Points correspond to landscapes and boxes correspond the range of cropland compositional and configurational heterogeneity sampled within each one of the eight regions (orange=Armorique, dark green=Camargue, dark blue=Coteaux, light blue=East Anglia, light red=Goettingen, light green=Lleida, pink=Ontario, dark red=PVDS). Cropland compositional heterogeneity corresponds to the Shannon index of crop diversity. Cropland configurational heterogeneity corresponds to the total length of crop borders measured in meters.

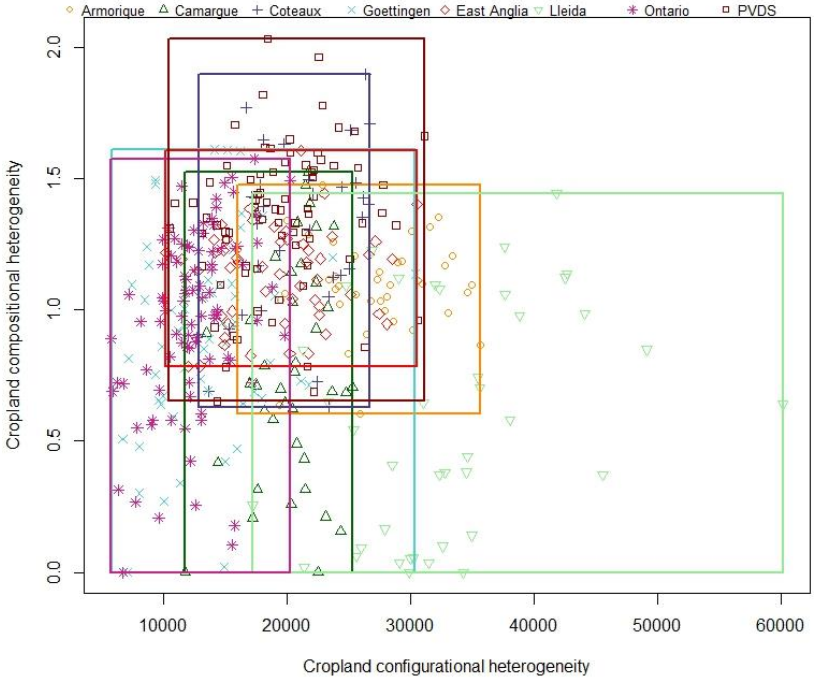


Figure 4. Conceptual representation of the two levels of analyses of the effect of crop heterogeneity on biodiversity: 1) across regions (a. linear effect, b. interactive effect and c. non-linear effect) 2) within regions (a. regional effect on intercept and b. regional effect on intercept and slope). Each point corresponds to a landscape. Points of different colours represent landscapes from different hypothetical regions. Grey lines correspond to the effect across regions, i.e. considering that the eight regions represent one single gradient. Lines of different colours correspond to the effect within hypothetical regions, i.e. considering that the eight regions are random replicates of the gradient. Details on statistical models corresponding to these five types of models are available in Appendix 4.

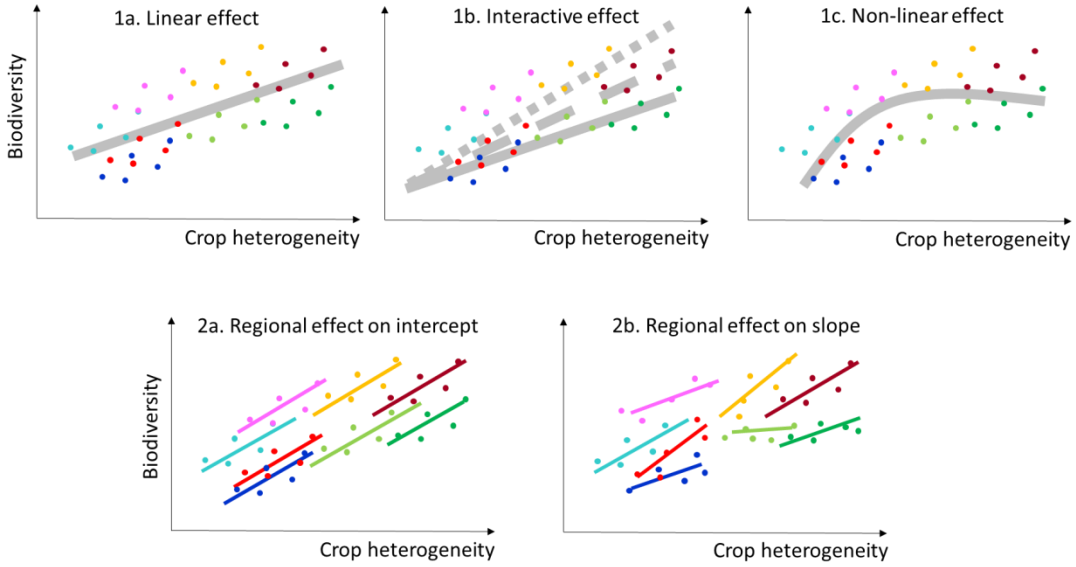
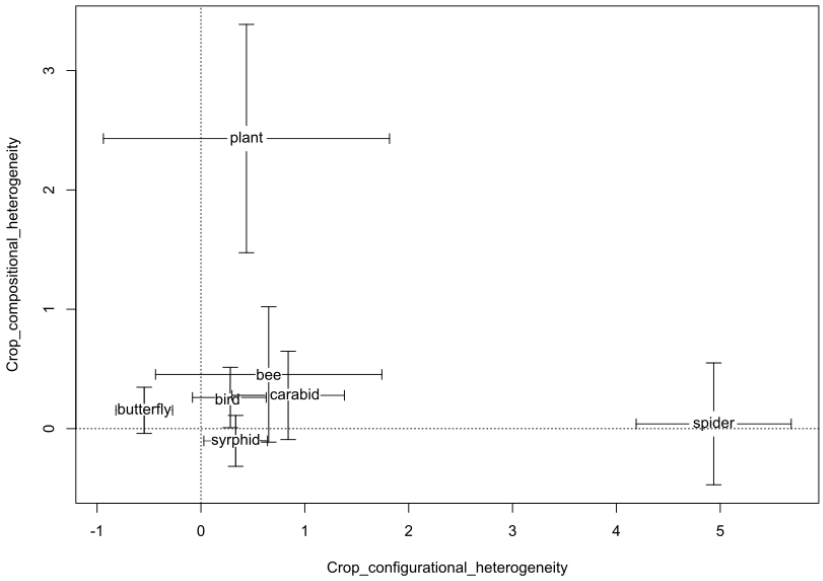
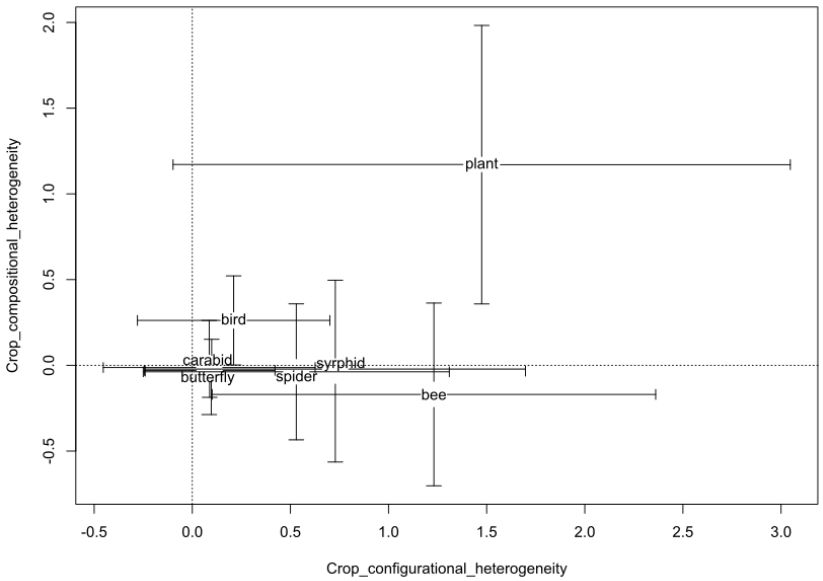


Figure 5. Effects of crop compositional and configurational heterogeneity on alpha diversity across taxa when considering: 1) a single gradient across regions (i.e. a linear model with no region effect) and 2) replicated gradients within regions (i.e. mixed model with a random effect of region on intercept). Each cross represents the mean effect and 95% confidence interval for each taxa.

1) Single gradient across regions



2) Replicated gradients within regions



Discussion

Significant effect of crop heterogeneity independent of semi-natural habitats across regions

This study provides the first large-scale assessment of the effect of cropland configurational and compositional heterogeneity, independently from the effect of semi-natural habitats, on multiple taxa across ecoregions, countries and landscape types. Our most important finding is that increasing cropland configurational and compositional heterogeneity while keeping the amount and distribution of semi-natural habitats constant can have a positive effect on biodiversity. This suggests that the heterogeneity-diversity relationship classically studied based on the amount of semi-natural habitats holds true even for more disturbed habitats such as crops. Testing the effect of cropland heterogeneity per se was only possible after taking into account both the amount and spatial distribution of semi-natural habitats (Concepción *et al.* 2012) and therefore required a huge amount of GIS and field work. It is important to mention that we could not avoid a certain level of correlation between cropland configurational and the length of semi-natural boundaries, especially in 'bocage' regions such as Armorique. However, the fact that we obtained similar results even when using only a subset of landscapes for which there was correlation was maintained below 0.4 within and across regions (see Appendix 4) confirm that this first main finding is very robust.

Our results were globally consistent both across and within regions for most taxa (Figure 5-1 and 5-2). Moreover, we found no evidence for regional differences in the effects of cropland configurational and compositional heterogeneity on alpha diversity (except for butterfly; Table 1). Our study therefore suggests that relationships between cropland heterogeneity and biodiversity are consistent across ecoregions, countries and landscape types. It also suggest that the range of crop heterogeneity currently observed within regions may limit our ability to detect the effect of cropland heterogeneity on biodiversity. This undeniably confirms the absolute need to conduct multi-region studies with common protocols in order to disentangle the effect of landscape variables on biodiversity.

Complementary effects of cropland configurational and compositional heterogeneity across taxa

An important finding of our study is that both cropland compositional and configuration heterogeneity have a significant effect on biodiversity, independently of each other, and that each component of cropland heterogeneity influences different sets of taxa.

Cropland configurational heterogeneity had a significant effect on butterfly, carabid, spider and syprhid diversity. The positive effect on carabid, spider and syprhid as well as the presence of significant non-linear effects support Hyp 2c (Box 1) for these taxa. Our results therefore suggest that variations within the range of cropland configurational heterogeneity currently observed in western European and North American agricultural landscapes, with an average field size of 2,98 ha ± 1.99 sd, are sufficient to have a significant impact on most arthropod taxa. The fact that we did not detect any effect of cropland configurational heterogeneity on bird, bee and plant is likely to be explained by the high mobility of bird and bee or the lack of mobility for plant but it may also be explained by interactions between cropland configurational heterogeneity and covariates (e.g. woody cover, practices). These results are consistent with previous studies showing that mean field size do not affect weed assemblages (Marshall 2009), but contrast with other studies showing that smaller mean field sizes are associated with higher herbaceous plant diversity in wheat fields (Gaba *et al.* 2010). The fact that we obtained similar results even when running models at the sampling site scale and adding crop type as a covariate (results not shown) suggests that our results are robust. Further analyses on these taxa should allow us to better understand the potential effect of cropland configurational heterogeneity on bird and plant diversity.

The positive effect of cropland compositional heterogeneity on bird and plant as well as the absence of significant non-linear effects support Hyp 1a (Box 1) for these taxa. The positive effect of cropland compositional heterogeneity on bird is consistent with other studies showing that increasing crop diversity can benefit bird diversity (Firbank *et al.* 2008; Lindsay *et al.* 2013). The positive effect of cropland compositional heterogeneity on plant is consistent with the high degree of specialization of weed communities depending on crop types (Andreasen, Streibig & Haas 1991; Marshall 2009). Finally, the significant and positive interaction between cropland compositional and cropland configurational heterogeneity for syrphid suggests that increasing cropland compositional heterogeneity may not have a direct effect but may nevertheless benefit biodiversity indirectly by emphasizing the effect of cropland configurational heterogeneity.

Implications for biodiversity management in agricultural systems

Our study shows that managing the crop mosaic while maintaining the amount and spatial distribution of semi-natural habitats can benefit biodiversity both across taxa and regions. In the current context of repeated criticisms of current agricultural policies (Pe'er *et al.* 2014), our findings represent a first step towards a valuable new path for biodiversity conservation in agricultural landscapes. Although the crop mosaic is under constraints such as land property, hydrology or topography, managing the crop mosaic is likely to be less constraining than creating new semi-natural habitats. Developing new agricultural policies based on the role of cropland heterogeneity will require further research, in particular regarding the perception of farmers or the potential benefits cropland heterogeneity may have on ecosystem services such as pest control and crop pollination which could ultimately contribute to food production.

Acknowledgments

This research was funded by the ERA-Net BiodivERsA, with the national funders French National Research Agency (ANR-11-EBID-0004), German Ministry of Research and Education, German Research Foundation and Spanish Ministry of Economy and Competitiveness, part of the 2011 BiodivERsA call for research proposals. The UK component of this research was funded by the UK Government Department of the Environment, Food and Rural Affairs (Defra), as project WC1034. The Canada component of this research was funded by the Natural Sciences and Engineering Research Council of Canada (NSERC), 99 Strategic Project grant, the Canada Foundation for Innovation, Environment Canada (EC), and Agriculture and Agri-Foods 101 Canada (AAFC). We would also like to thank the many farmers and farm owners from all eight regions who graciously permitted us to work on their lands. In addition to the co-authors, the project involved direct assistance from more than 150 individuals for geomatic analyses, field sampling, and species identification. We would like to thank all of them for their huge contribution to the FarmLand project and this study.

Cited References

Allouche, O., Kalyuzhny, M., Moreno-Rueda, G., Pizarro, M. & Kadmon, R. (2012) Area–heterogeneity tradeoff and the diversity of ecological communities. *Proceedings of the National Academy of Sciences*.

Andreasen, C., Streibig, J.C. & Haas, H. (1991) Soil properties affecting the distribution of 37 weed species in Danish fields. *Weed Research*, **31**, 181–187.

Andren, H., Delin, A. & Seiler, A. (1997) Population response to landscape changes depends on specialization to different landscape elements. *Oikos*, **80**, 193–196.

Benton, T.G., Vickery, J.A. & Wilson, J.D. (2003) Farmland biodiversity: is habitat heterogeneity the key? *Trends Ecol. Evol.*, **18**, 182–188.

Bibby, C.J., Hill, D.A., Burgess, N.D. & Mustoe, S., (first). (2005) *Bird Census Techniques*. Academic Press, London, UK.

Burton, R.J.F., Kuczera, C. & Schwarz, G. (2008) Exploring Farmers' Cultural Resistance to Voluntary Agri-environmental Schemes. *Sociologia Ruralis*, **48**, 16–37.

Butler, S.J., Vickery, J.A. & Norris, K. (2007) Farmland Biodiversity and the Footprint of Agriculture. *Science*, **315**, 381–384.

Concepción, E.D., Díaz, M., Kleijn, D., Báldi, A., Batáry, P., Clough, Y., Gabriel, D., Herzog, F., Holzschuh, A., Knop, E., Marshall, E.J.P., Tscharntke, T. & Verhulst, J. (2012) Interactive effects of landscape context constrain the effectiveness of local agri-environmental management. *Journal of Applied Ecology*, **49**, 695–705.

Danielson, B.J. (1991) Communities in a Landscape: The Influence of Habitat Heterogeneity on the Interactions between Species. *The American Naturalist*, **138**, 1105–1120.

Donald, P.F., Green, R.E. & Heath, M.F. (2001) Agricultural intensification and the collapse of Europe's farmland bird populations. *Proceedings of the Royal Society of London B.*, **268**, 25–29.

Dunning, J.B., Danielson, B.J. & Pulliam, H.R. (1992) Ecological Processes That Affect Populations in Complex Landscapes. *Oikos*, **65**, 169–175.

Fahrig, L., Baudry, J., Brotons, L., Burel, F.G., Crist, T.O., Fuller, R.J., Sirami, C., Siriwardena, G.M. & Martin, J.-L. (2011) Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecology letters*, **14**, 101–112.

Firbank, L.G., Petit, S., Smart, S., Blain, A. & Fuller, R.J. (2008) Assessing the impacts of agricultural intensification on biodiversity: a British perspective. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, **363**, 777–787.

Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N. & Snyder, P.K. (2005) Global Consequences of Land Use. *Science*, **309**, 570–574.

Gaba, S., Chauvel, B., Dessaint, F., Bretagnolle, V. & Petit, S. (2010) Weed species richness in winter wheat increases with landscape heterogeneity. *Agriculture, Ecosystems & Environment*, **138**, 318–323.

Gregory, R.D., G. Noble, D. & Custance, J. (2004) The state of play of farmland birds: population trends and conservation status of lowland farmland birds in the United Kingdom. *Ibis*, **146**, 1–13.

Hawro, V., Ceryngier, P., Tscharntke, T., Thies, C., Gagic, V., Bengtsson, J., Bommarco, R., Winqvist, C., Weisser, W.W., Clement, L.W., Japoshvili, G. & Ulrich, W. (2015) Landscape complexity is not a major trigger of species richness and food web structure of European cereal aphid parasitoids. *BioControl*, **60**, 451–461.

Henderson, I.G., Vickery, J.A. & Carter, N. (2004) The use of winter bird crops by farmland birds in lowland England. *Biological Conservation*, **118**, 21–32.

Holzschuh, A., Dormann, C.F., Tscharntke, T. & Steffan-Dewenter, I. (2013) Mass-flowering crops enhance wild bee abundance. *Oecologia*, **172**, 477–484.

Holzschuh, A., Steffan-Dewenter, I. & Tscharntke, T. (2010) How do landscape composition and configuration, organic farming and fallow strips affect the diversity of bees, wasps and their parasitoids? *The Journal of Animal Ecology*, **79**, 491–500.

Krebs, J.R., Wilson, J.D., Bradbury, R.B. & Siriwardena, G.M. (1999) The second Silent Spring? *Nature*, **400**, 611–612.

Lindsay, K.E., Kirk, D.A., Bergin, T.M., Best, L.B., Sifneos, J.C. & Smith, J. (2013) Farmland Heterogeneity Benefits Birds in American Mid-west Watersheds. *The American Midland Naturalist*, **170**, 121–143.

Marshall, E.J.P. (2009) The impact of landscape structure and sown grass margin strips on weed assemblages in arable crops and their boundaries. *Weed Research*, **49**, 107–115.

Miyashita, T., Chishiki, Y. & Takagi, S.R. (2012) Landscape heterogeneity at multiple spatial scales enhances spider species richness in an agricultural landscape. *Population Ecology*, **54**, 573–581.

Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Loucks, C.J., Allnutt, T.F., Ricketts, T.H., Kura, Y., Lamoreux, J.F., Wettengel, W.W., Hedao, P. & Kassem, K.R. (2001) Terrestrial Ecoregions of the World: A New Map of Life on Earth A new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. *BioScience*, **51**, 933–938.

Pasher, J., Mitchell, S., King, D., Fahrig, L., Smith, A. & Lindsay, K. (2013) Optimizing landscape selection for estimating relative effects of landscape variables on ecological responses. *Landscape Ecology*, **28**, 371–383.

Pe'er, G., Dicks, L.V., Visconti, P., Arlettaz, R., Báldi, A., Benton, T.G., Collins, S., Dieterich, M., Gregory, R.D., Hartig, F., Henle, K., Hobson, P.R., Kleijn, D., Neumann, R.K., Robijns, T., Schmidt, J., Shwartz, A., Sutherland, W.J., Turbé, A., Wulf, F. & Scott, A.V. (2014) EU agricultural reform fails on biodiversity. *Science*, **344**, 1090–1092.

Perović, D., Gámez-Virués, S., Börschig, C., Klein, A.-M., Krauss, J., Steckel, J., Rothenwöhrer, C., Erasmi, S., Tscharntke, T. & Westphal, C. (2015) Configurational landscape heterogeneity shapes functional community composition of grassland butterflies. *Journal of Applied Ecology*, **52**, 505–513.

Poggio, S.L., Chaneton, E.J. & Ghersa, C.M. (2010) Landscape complexity differentially affects alpha, beta, and gamma diversities of plants occurring in fencerows and crop fields. *Biological Conservation*, **143**, 2477–2486.

Raymond, L., Sarthou, J.-P., Plantegenest, M., Gauffre, B., Ladet, S. & Vialatte, A. (2014) Immature hoverflies overwinter in cultivated fields and may significantly control aphid populations in autumn. *Agriculture, Ecosystems & Environment*, **185**, 99–105.

Robertson, G.P., Gross, K.L., Hamilton, S.K., Landis, D.A., Schmidt, T.M., Snapp, S.S. & Swinton, S.M. (2014) Farming for Ecosystem Services: An Ecological Approach to Production Agriculture. *BioScience*, biu037.

Roschewitz, I., Gabriel, D., Tscharntke, T. & Thies, C. (2005) The effects of landscape complexity on arable weed species diversity in organic and conventional farming. *Journal of Applied Ecology*, **42**, 873–882.

Stein, A., Gerstner, K. & Kreft, H. (2014) Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecology Letters*, **17**, 866–880.

Tilman, D., Fargione, J., Wolff, B., D'Antonio, C., Dobson, A., Howarth, R., Schindler, D., Schlesinger, W.H., Simberloff, D. & Swackhamer, D. (2001) Forecasting agriculturally driven global environmental change. *Science (New York, N.Y.)*, **292**, 281–284.

Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I. & Thies, C. (2005) Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. *Ecology Letters*, **8**, 857–874.

Tscharntke, T., Tylianakis, J.M., Rand, T.A., Didham, R.K., Fahrig, L., Batáry, P., Bengtsson, J., Clough, Y., Crist, T.O., Dormann, C.F., Ewers, R.M., Fründ, J., Holt, R.D., Holzschuh, A., Klein, A.M., Kleijn, D., Kremen, C., Landis, D.A., Laurance, W., Lindenmayer, D., Scherber, C., Sodhi, N., Steffan-Dewenter, I., Thies, C., van der Putten, W.H. & Westphal, C. (2012) Landscape moderation of biodiversity patterns and processes - eight hypotheses. *Biological Reviews*, **87**, 661–685.

Winqvist, C., Ahnström, J. & Bengtsson, J. (2012) Effects of organic farming on biodiversity and ecosystem services: taking landscape complexity into account. *Annals of the New York Academy of Sciences*, **1249**, 191–203.

List of Appendixes

Appendix 1 – Region and landscape selection methods

Region selection

We selected eight agricultural regions that belong to six different ecoregions (as defined in Olson *et al.* 2001) : Eastern Great Lakes lowland forests (Ontario), Celtic broadleaf forests and English lowland beech forests (East Anglia), Atlantic mixed forests (Armorique, Plaine et Val de Sèvre), Western European broadleaf forests (Goettingen, Coteaux de Gascogne), Iberian sclerophyllous and semi-deciduous forests (Lleida) and Northeastern Spain & Southern France Mediterranean forests (Camargue). Topography varied from flat (e.g. Camargue, Eastern Ontario) to intermediate (e.g. Goettingen, Lleida), to hilly (e.g. Coteaux de Gascogne); climate varied from dry (e.g. Lleida) to humid (e.g. East Anglia); complexity in crop field shapes varied from rectilinear (e.g. Camargue, Eastern Ontario) to intermediate complexity (e.g. Coteaux de Gascogne, Armorique) to complex field shapes (e.g. Lleida); and diversity of crop types varied from low (e.g. Camargue, Lleida) to high (e.g. Coteaux de Gascogne). Specific agricultural products were also found in some regions, e.g. dairy (Armorique), olives (Lleida) or rice (Camargue).

Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Loucks, C.J., Allnutt, T.F., Ricketts, T.H., Kura, Y., Lamoreux, J.F., Wettengel, W.W., Hedao, P. & Kassem, K.R. (2001) Terrestrial Ecoregions of the World: A New Map of Life on Earth A new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. BioScience, 51, 933–938.

Landscape selection

The purpose of the landscape selection protocol was to select in each region a set of landscapes in a pseudo-experimental design (also called a "mensurative experiment") in which we attempt to isolate the predictor variables of interest, i.e. obtain two independent gradients (compositional heterogeneity and configurational heterogeneity of the cropped portions of the landscapes) while controlling for confounding variables (amount of semi-natural cover, organic farms). The general protocol is detailed in (Pasher *et al.* 2013).

We used the highest resolution and most recent remotely sensed data or the best land cover map available. We delineated all crop fields (contiguous production cover), even when adjacent fields contain the same crop type (as they may belong to different farmers or may be managed differently). We attributed each crop field to one of the 34 crop cover types from the following list: cereal, fallow, alfalfa, clover, ryegrass, grassland, rice, corn, sunflower, sorghum, millet, moha, oilseed rape, mustard, pea, bean, soybean, linseed, orchard, almond, olive, vineyard, mixed vegetables, sugar beet, asparagus, carrot, onion, parsnip, potato, tomato, melon, strawberry, raspberry, wild bird cover. We also delineated patches of non-crop cover types (woodland, open land, wetland and built-area).

We selected 1 km x 1 km landscapes associated with the smallest ranges of variation in crop cover within each region (e.g. 70 to 90%) but avoiding the 100% zone – if possible. We calculated cropland compositional heterogeneity (crop Shannon diversity index) and cropland configurational heterogeneity (crop total border length or mean field size) using simple and common metrics with relatively well-known statistical properties. We then selected a set of landscapes spatially independent, representing the maximum variation for both cropland compositional heterogeneity and cropland configurational heterogeneity. Finally, we selected a subset of landscapes in order to obtain two independent gradients of cropland compositional heterogeneity and cropland configurational heterogeneity.

The number of landscapes selected in each region is provided in Table A4.1 in Appendix 4.

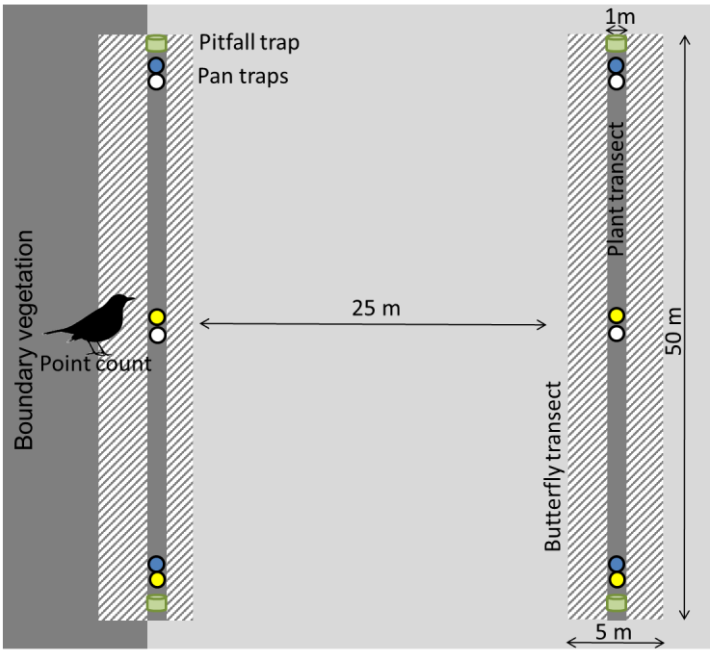
Pasher, J., Mitchell, S., King, D., Fahrig, L., Smith, A. & Lindsay, K. (2013) Optimizing landscape selection for estimating relative effects of landscape variables on ecological responses. Landscape Ecology, 28, 371–383.

Appendix 2 – Sampling site selection and biodiversity sampling methods

Sampling site selection

Within each landscape of 1 x 1 km we selected three sampling sites. They were located in field boundaries between two crop fields, at least 200 m apart, at least 50 m from the border of the 1km x 1km landscape, and at least 50 m from non-crop habitat patches such as forests. We tried as much as possible to select boundaries with similar vegetation within each region (i.e. only grassy boundaries or hedgerows). If not possible, we selected a set of boundary types in order to avoid correlations between boundary vegetation type and cropland compositional/configurational heterogeneity. At each point selected above, one of the adjoining crop fields was chosen as the field to be sampled. Within these constraints, we tried to select sampling sites based on the dominant crop types within each region. For example, in Goettingen, we sampled two wheat fields and one grassland in each landscape. When this was not feasible, we selected sampling sites based on crop types available within a given landscape, trying to avoid correlation between crop type sampled and the two cropland heterogeneity gradients as much as possible.

Figure A2.1. Biodiversity sampling design within each sampling site



Plant

Plant surveys were conducted along two 1m wide and 50m long transects, in the field border and the field interior. Each transect was divided in quadrats to facilitate the survey. In all regions, a minimum of 20 m² were sampled per transect. In Ontario, transects were 2m wide and the field border transect included both the field border vegetation and the boundary vegetation. Surveys were conducted once, except in Ontario, Goettingen and East Anglia were surveys were conducted twice.

Pollinator (bee and syrphid)

Bees and syrphids were sampled using colored pan traps. Plastic bowls painted in blue, white or yellow were placed in pairs at each end and at the center of each transect. As a result, we used six pan traps per transect, 12 pan traps per sampling site and 36 pan traps per landscape. The height of pan traps was adjusted to vegetation height. Cups were filled with water, with three drops of soap added per 1L of water. The traps were left in the field for four days, the insects were then stored in 70 % ethanol and later identified to species level. Pollinators sampling was carried out twice during the growing season (April-July), dates being adjusted in each region based on regional climatic conditions. In Ontario the syrphid dataset was obtained from sweep-netting along the two transects rather than trapping.

Predator (carabid and spider)

Carabids and spiders were sampled using pitfall traps. Cups were half-filled with a solution of 10 drops of soap and 10 g of salt per 1L of water and placed in the ground. One trap was placed at each end of each transect (two traps per transect and four per sampling site in total). The traps were left in the field for four days, the insects were then stored in 70 % ethanol and later identified to species level. Predator sampling was carried out twice during the growing season (April-July), dates being adjusted in each region based on regional climatic conditions. Predator sampling was carried out only once in East Anglia in 2012 due to bad weather conditions and could not be conducted in rice fields in Camargue due to the presence of water.

Butterfly

Butterfly surveys were conducted along two 5m wide and 50m long transects, in the field border and the field interior. Surveys were conducted on calm (Beaufort scale < 3), sunny days, when the temperature was > 15°C. The observer recorded all butterfly species observed within an imaginary 5 m-side box (2.5 m to each side, 5 m in front and 5 m high) during approximately 10 min per transect (Pollard and Yates 1993). Individuals which could not be identified by sight were captured with a butterfly net for closer examination (time was stop).

Pollard, E., Yates, T.J. (Eds.), 1993. Monitoring butterflies for ecology and conservation. Chapman et Hall, London.

Bird

Birds were surveyed using 10-minutes point counts (Bibby *et al.* 2005) located at the center of the border transect. All individuals singing or seen within a distance of 0-100m were recorded. Birds flying across were considered as transients and thus not included. Counts were conducted twice, except in East Anglia in 2012 due to bad weather conditions and in rice fields in Camargue due to the specific phenology of this crop type. Surveys were conducted during the peak season, between April and June depending on the region, and during peak activity hours, from 1 to 4 hours after sunrise and under good weather conditions.

Bibby, C.J., Hill, D.A., Burgess, N.D. & Mustoe, S., (first). (2005) Bird Census Techniques. Academic Press, London, UK.

Appendix 3 – Cropland heterogeneity and covariates calculation methods

Landscape mapping

Each landscape was mapped based on remote-sensed data and ground-truthing. All crop fields, boundaries between two crop fields, non-agricultural habitat patches were mapped (See Fig. A3.1). Crop types included: cereal, fallow, alfalfa, clover, ryegrass, grassland, rice, corn, sunflower, sorghum, millet, moha, oilseed rape, mustard, pea, bean, soybean, linseed, orchard, almond, olive, vineyard, mixed vegetables, sugar beet, asparagus, carrot, onion, parsnip, potato, tomato, melon, strawberry, raspberry, wild bird cover. Non-agricultural cover types included: woodland, open land, wetland and built-area. Boundary types included: woody, grassy, bare ground, track and watery.

Figure A3.1. Example of land cover map used to calculate crop heterogeneity variables for each landscape.

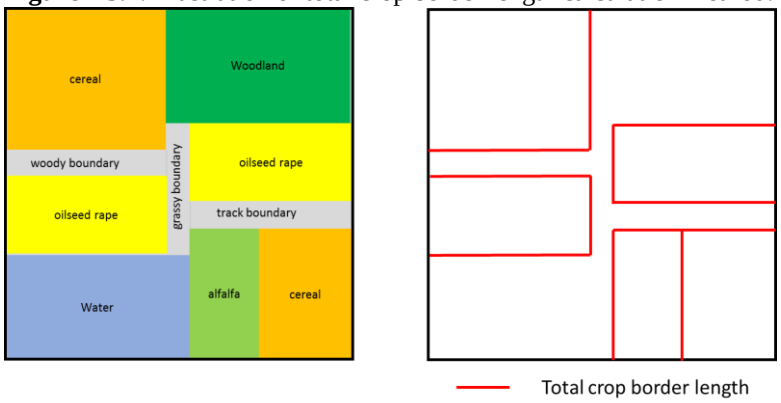
Cropland compositional heterogeneity

Cropland compositional heterogeneity was measured based on crop taxonomic diversity i.e. all crops were considered equally different. We chose to use the Shannon diversity index because it is a widely used metrics. We calculated this index as $H' = -\sum_{i=1}^{n} p_i \ln p_i$ where p_i is the proportion of crop type i in the landscape.

Cropland configurational heterogeneity

Cropland configurational heterogeneity was measured based on total crop border length, measured in meters. We chose to use this metric over metrics such as crop mean field size because it is less influenced by the grain size of the landscape. Total crop border length was calculated as the sum of perimeters of all crop fields minus the length of fields artificially created by intersection of the 1km x 1km landscape (see Fig. A3.2). This means that both crop/crop and crop/non-crop borders were included in the calculation of total crop border length. It is important to note that total crop border length is a measure of cropland configurational heterogeneity, not a measure of the length of boundary vegetation (e.g. hedgerows, grassy margins). As a result, although internal boundaries were sometimes observed within crop fields (for example in Lleida) and do increase the amount of semi-natural habitat and boundary length, they do not increase cropland configurational heterogeneity and were therefore not included in the calculation of crop total border length.

Figure A3.2. Illustration of total crop border length calculation method.



Covariates

The percentage of semi-natural habitat in the landscape was calculated as the sum of woodland, open land and wetland cover in the landscape. The length of semi-natural boundaries in the landscape was calculated as the half the sum of perimeters of woody, grassy, bare ground and watery boundaries in the landscape.

Appendix 4 – Description of variables and statistical analyses

1. Description of explanatory and response variables

Table A4.1. Correlations across and within regions among explanatory variables (SHDI = crop compositional heterogeneity, TBL= crop configurational heterogeneity, SNC=semi-natural cover, SNB=semi-natural boundary).

	SHDI-TBL	SHDI-SNC	TBL-SNB	Nb landscapes
Correlation across all regions	0.01	-0.28	0.71	435
Armorique	-0.003	0.09	0.83	40
Camargue	0.19	-0.25	0.93	40
Coteaux	0.32	-0.22	0.78	32
EastAnglia	0.25	0.06	0.69	60
Goettingen	0.13	0.15	0.51	52
Lleida	0.33	-0.14	0.85	40
Ontario	0.4	-0.13	0.82	93
PVDS	0.17	-0.08	0.51	78
Max correlation within a region	0.4	-0.25	0.93	

Table A4.2. Mean alpha diversity per taxa and correlations between variable responses (mean alpha diversity per landscape).

	Mean alpha	bird	bee	butterfly	carabid	plant	spider
bird	5.61±2.24						
bee	9.71±3.92	0.03					
butterfly	3.55±1.90	-0.05	0.08				
carabid	7.74±4.69	-0.06	-0.17	0.25			
plant	23.29±9.91	0.21	-0.19	0.16	-0.26		
spider	13.54±6.04	0.11	0.41	-0.17	0.36	-0.46	
syrphid	4.14±1.81	-0.08	0.27	-0.15	0.11	-0.01	0.21

2. Statistical analyses

Analyses were performed in *R 3.2.5*. Linear models were fitted using the function *lm* and *lmer* in the package *lme4*.

2.1. Testing our hypotheses

We addressed the following questions: (i) what are the relative effects of farmland compositional heterogeneity, farmland configurational heterogeneity and the amount of semi-natural habitat on biodiversity? (ii) are these effects independents from each other? (iii) are these effect non-linear? and (iv) are these effects consistent across regions?

First, we built models with no region effect to test for linear effects, interactions between effects and quadratic effects (see Figure 4 - 1a,b,c):

1a) lm (Response ~ scale(Crop_SHDI) + scale(Crop_TBL) + scale(Seminat_Cover) + scale(Seminat_boundary_m))
1b) lm (Response ~ scale(Crop_SHDI) * scale(Crop_TBL) + scale(Seminat_Cover) + scale(Seminat_boundary_m))
1c) lm (Response ~ scale(Crop_SHDI) + scale(Crop_TBL) + scale(Crop_SHDI)² + scale(Crop_TBL)² + scale(Seminat_Cover) + scale(Seminat_boundary_m))

Second, we built models with region as a random effect on intercept (Figure 4 – 2a):

2a) lmer (Response ~ scale(Crop_SHDI) + scale(Crop_TBL) + scale(Seminat_Cover) + scale(Seminat_boundary_m) + (1|Region))

Finally, we built models with region as a random effect on both intercept and slope (Figure 4 - 2b):

2b) lmer (Response ~ scale(Crop_SHDI) + scale(Crop_TBL) + scale(Seminat_Cover) + scale(Seminat_boundary_m) + (1 + (scale(Crop_TBL) + scale(Crop_SHDI)) | Region))

2.2. Assessing potential methodological concerns

We also addressed three potential methodological concerns associated with our sampling design and the use of mixed models.

First, we compared model outputs between models 1a) and models at the sampling site level, with crop type as a covariate:

1d) glmer (Response ~ scale(Crop_SHDI) + scale(Crop_TBL) + scale(Seminat_Cover) + scale(Seminat_boundary_m) + Crop_category + (1 | Landscape), family='poisson')
Results were consistent when considering either model 1a) or 1d) for all taxa.

Second, we compared model outputs between models where region was considered as a random effect (2a) and models where region was considered as a fixed effect (2a bis):

2a bis) lm (Response ~ scale(Crop_SHDI) + scale(Crop_TBL) + scale(Seminat_Cover) + scale(Seminat_boundary_m) + Region)
Results were consistent when considering either model 2a) or 2c) for all taxa.

Third, we compared model outputs between models built with the whole dataset (435 landscapes) and models built with a subset of landscapes where correlation between explanatory variables and covariates is controlled for, both across and within regions. To achieve this, we selected a subset of landscapes where correlation between explanatory

variables remains below 0.4 both across and within each region, with a constraint of at least 20 landscapes per region.
We obtained a subset with the following characteristics.

Table A4.3. Correlations across and within regions among the variables of interest and covariates (SHDI = crop compositional heterogeneity, TBL= crop configurational heterogeneity, SNC=semi-natural cover, SNB=semi-natural boundary) for the landscape subset.

	SHDI-TBL	SHDI-SNC	TBL-SNB	Nb landscapes
Correlation across all regions	0.04	-0.31	0.4	274
Armorique	-0.02	0.28	0.3	20
Camargue	0.25	-0.19	0.39	20
Coteaux	-0.29	-0.38	0.26	20
EastAnglia	0.32	-0.19	0.32	43
Goettingen	0.18	0.1	0.3	45
Lleida	0.06	0.08	0.06	20
Ontario	0.24	-0.07	0.36	44
PVDS	0.13	-0.15	0.23	62
Max correlation within region	0.32	-0.38	0.39	

Results were consistent when considering either the full dataset or the subset of landscapes for all taxa.

These three complementary tests confirmed that our approach was robust and independent of residual correlation between covariates or methodological choices.

CHAPTER 2
Configurational and compositional heterogeneity of farmland affect flower-visitor and ground-dwelling arthropod traits across Europe

Article in preparation

Aliette Bosem Baillod*, Annika Hass *, Péter Batáry, Yann Clough, Clélia Sirami, Jean-Louis Martin, Lenore Fahrig, Audrey Alignier, Mª Ángeles Marcos, Jose Antonio Barrientos, Jacques Baudry, Colette Bertand, Gerard Bota, Vincent Bretagnolle, Lluis Brotons, Françoise Burel, Romain Carrié, Gaetan Lefebvre, Romain Georges, Bertrand Gauffre, David Giralt, Nicolas Gross, Samuel Hilaire, Jesus Minano, Annie Ouin, Brigitte Poulin, Antonio Ricarte, Alexis Saintilan, Gavin Siriwardena, Teja Tscharntke

* Equally contributing authors

Authorship

A.B.B. and A.H equally wrote the manuscript and analysed data. A.B.B. and A.H with help of P.B., T.T and Y.C. developed the concept of this manuscript. All authors contributed to revisions. C.S., L.F. and J.M. coordinated the EU project. A.B.B, J.A.B and A.S. compiled carabid and spider trait data. A.H. compiled butterfly and hoverfly trait data. A.B.B and A.S partly performed field work. All authors contributed to the study methodology and/or performed field work and species identification.

Abstract

Biodiversity conservation in agricultural landscapes has mainly focused on maintenance and restoration of semi-natural habitats, while the heterogeneity of the crop mosaic itself has received much less attention. We aimed at disentangling the importance of configurational vs. compositional crop heterogeneity (smaller field size vs. crop diversity) as well as semi-natural habitat cover on the local and landscape scale trait filtering of flower-visiting and ground-dwelling arthropods. We used partial RLQ analysis to test the effects on body size, dispersal, foraging and reproduction traits in seven European regions.
Proximity to field borders was the most important factor shaping functional diversity. In addition, crop configurational heterogeneity promoted butterflies and carabids with high feeding specialization, while high crop compositional heterogeneity supported hoverflies with low reproduction potential as well as generalist spiders. We conclude that small-scale farming and crop diversification are neglected agri-environmental measures to promote functional diversity of arthropods providing important ecosystem services such as biological control and pollination.

Keywords: crop diversity, field size, edge effect, hoverfly, butterfly, carabid beetle, spider, partial RLQ

Introduction

Arthropods provide essential ecosystem services in agricultural landscapes such as pollination and biocontrol (Klein *et al.* 2007; Tscharntke *et al.* 2007). However, insect diversity and abundance are declining worldwide, which risks undermining the stability of ecosystem service provision for crop production in the future (Dirzo *et al.* 2014; Newbold *et al.* 2015). There is clear evidence that semi-natural habitats at local and landscape scale such as hedges, unimproved grasslands and flower strips have a positive effect on arthropods in farmland across taxa and geographic regions (Hendrickx *et al.* 2007; Billeter *et al.* 2008; Garibaldi *et al.* 2011). However, Fahrig *et al.* (2011) question the traditional way of considering only semi-natural areas as valuable habitats for conservation and the crop production area as a homogenous 'hostile matrix'. Indeed, meta-analyses have demonstrated that matrix characteristics are most important for predicting species distribution in fragmented landscapes (Prugh *et al.* 2008; Watling *et al.* 2011). Therefore, enhancing crop heterogeneity at the landscape scale could provide different resources and structures in agricultural systems that promote biodiversity and ecosystem services without taking land out of production (Fahrig *et al.* 2011). There are two different types of crop heterogeneity: Crop compositional heterogeneity includes the diversity of crop types grown in a landscape, whereas crop configurational heterogeneity describes their spatial arrangement, e.g. mean field size (Fahrig *et al.* 2011). Different crops are expected to provide various food resources which can enhance insect species diversity (Palmu *et al.* 2014) and contrasting abiotic conditions in crops have been shown to promote or prevent animal dispersal (Cosentino *et al.* 2011). The spatial crop arrangement could also play an important role by increasing resource availability through higher interspersion and providing more edge habitats (Fahrig *et al.* 2011). It is well known that species in agricultural landscape move from crops to other habitat types and vice versa (Blitzer *et al.* 2012), emphasizing the potential importance of landscape-scale crop heterogeneity, but so far its influence on biodiversity has largely been neglected.

In agro-ecosystems, not only species richness and abundance, but also functional diversity is affected by land use change and may impair ecosystem functions and services (Tscharntke *et al.* 2008; Wood *et al.* 2015). Studies addressing how species trait composition is affected on local and landscape scales in farming systems focused mainly on the role of semi-natural habitats. On the local scale, habitat patch size is an important predictor for community trait composition of insects (Steffan-Dewenter & Tscharntke 2000; Bommarco *et al.* 2010; Öckinger *et al.* 2010), but the importance of local habitat quality achieved much less attention. However, increasing local management intensity can have negative effects on butterflies with low dispersal ability, a low number of generations and a short flight period (Börschig *et al.* 2013). There is little evidence how species traits change on local scale with management changes in annual crops, but phytophagous carabids and Heteroptera with a low reproduction potential prefer field borders compared to field interiors (Birkhofer *et al.* 2014). This indicates the potential importance of field borders for functionally diverse insect communities, but studies across different taxa and regional contexts are missing so far.

On the landscape scale, habitat fragmentation is in the focus of most studies on species traits in agricultural systems. Body size and dispersal capacity (that are usually highly correlated) are expected to increase with fragmentation due to reduced connectivity of habitat patches (Hendrickx *et al.* 2009).

Furthermore, feeding specialists and species with low reproductive potential are negatively affected by high fragmentation, because they depend on large and well-connected habitats to fulfill their feeding requirements (Öckinger *et al.* 2010) or have difficulties to recolonize habitats after local extinction processes due to their low population growth (Henle *et al.* 2004).

Only recently, studies have aimed at disentangling the effects of landscape habitat composition and configuration of semi-natural habitats: Landscape scale habitat composition measured as the proportion of woodlands favoured apterous carabid beetles (Duflot *et al.* 2014), higher habitat diversity promoted feeding specialists across a wide range of arthropod taxa (Gámez-Virués *et al.* 2015), while configurational heterogeneity promotes species with small body sizes (Gámez-Virués *et al.* 2015) as well as butterflies with small body size, low dispersal ability and high feeding specialization (Perović *et al.* 2015). This supports the hypothesis that high configurational heterogeneity enhances landscape connectivity (Perović *et al.* 2015).

With a highly replicated data set, comprising 342 landscapes across seven contrasting regions in four different European countries, we investigated, to our knowledge, for the first time how trait community composition of two flower-visiting and two ground-dwelling arthropod taxa is influenced by local field conditions and landscape scale crop heterogeneity. On the local scale, we focused on field border versus interior effects, which are associated with different levels of plant species richness and flower cover. On the landscape scale, we aimed at disentangling the effects of crop composition, crop configuration and semi-natural habitats. We decided to consider four different traits that are available for most taxa and have been shown to be influenced by local and landscape environmental variables (Hendrickx *et al.* 2009; Öckinger *et al.* 2010; Gámez-Virués *et al.* 2015): Body size, foraging type, dispersal capacity and reproduction type. We expected novel insights how crop heterogeneity can complement traditional measures to support functionally diverse arthropod communities by testing the following hypotheses:

I) At the local scale, field borders are inhabited by species with small body size and low dispersal ability, because field margins are well connected. Additionally, we expect more herbivorous species in the field margin due spill over from the boundary vegetation that provides higher plant species richness (Birkhofer *et al.* 2014).

II) Landscape scale crop compositional heterogeneity affects mainly foraging traits. We assume that low crop compositional heterogeneity leads to more predatory arthropod communities, because more insect pests are expected in large monocultures (Veres *et al.* 2013).

III) Landscape scale crop configurational heterogeneity enhances connectivity due to more field borders, favouring species with low dispersal ability and small body size (Perović *et al.* 2015). Higher connectivity also benefits species with high feeding specialization and low reproduction rates (Henle *et al.* 2004).

IV) A high amount of semi-natural habitats at the landscape scale filters for small body sizes, feeding specialists and herbivores, as well as species with low dispersal and low reproduction ability due to high habitat quality, lower management-induced disturbance and high plant species richness.

Methods

Study area, landscape and site selection

We selected seven European regions in four different countries that differ substantially in climate and farming systems. In France sampling was conducted in Armorique, Camargue, Coteaux de Gascogne and Plaine et Val de Sèvre (PVDS). Additionally, we sampled in the Göttingen region in Germany, in East Anglia in the U.K., and in Lleida in Spain (for details see supplementary material, Fig. S1).

In each region we selected 1x1 km landscapes that represented orthogonal gradients of crop configuration and crop composition and we aimed at keeping the amount of semi-natural habitat as low as possible. Across all regions we selected 342 landscapes (Armorique:40, Camargue:40, Coteaux: 32, PVDS:78, Lleida:40, Göttingen:52, East Anglia:60). In each landscape, three fields of different crops were chosen for sampling. All fields in one landscape were situated at least 100 m apart from the landscape border and at least 200 m from each other. To keep crop type constant and ensure comparability between fields, all non-cereal fields were excluded from the analysis. This resulted in one or two fields per landscape and a total of 605 sampled fields.

Sampling

In all regions sampling was conducted in the cropping seasons 2013 and 2014 (only in East Anglia sampling took place in 2012 and 2013). Due to crop rotation different landscapes were chosen in the two sampling years. In each field we established two 50 m transects: One directly at the field border next to a semi-natural field margin and one interior transect, 25 m apart from the margin (Fig. S2). Pitfall traps with a diameter of 9.5 cm were installed at the endpoints of each transect (four traps per field) and filled with a solution of 10 drops of odourless dish soap and 10 g of salt per 1L water to sample carabid beetles and spiders. Hoverflies were caught with pan traps in three different colours: UV blue, UV yellow and white.

Six pan traps (two of each colour) were installed along each transect, in total 12 traps per field. Pan traps were filled with 500 ml water and a drop of odourless detergent; flower cover was estimated in a 3 m radius around each pan trap. Pitfall traps and pan traps were collected after four days in the field, all arthropods were stored in 70% ethanol and hoverflies, carabid beetles and spiders were identified to species level in the lab. There were two sampling rounds for each field.

Butterflies were sampled with transect walks along the same 50 m transects during warm, sunny and windless weather conditions. Transects were 5 m wide and during 10 min walks we recorded all butterflies along the transect area. Butterflies were caught with insect nets for species identification if necessary. Additionally, flower cover inside the transect area was estimated. There was one sampling round for butterflies in most regions, but in Lleida and East Anglia there were two.

Plant species richness was also recorded along the 50 m transects. Plant transects were 1 m wide and separated in ten 1x5m segments. In five of those segments all plant species, other than the sown crop were recorded. There was one visit for plant sampling in most regions, but two in Göttingen.

Local and landscape environmental variables

Local environmental variables included in the analysis were transect position (field border vs. interior), plant species richness for carabid beetles and spiders and flower cover for hoverflies and butterflies.
On the landscape scale, we included crop configuration, crop composition and the amount of semi-natural habitats (Table 1). Therefore, we conducted ground truthing for the sampled landscapes to record all crops grown in one landscape and to map all field boundary types. Then we calculated crop configuration as the total border length of all fields in the landscape (TBL) per total crop area (m/ha). Crop composition was calculated as the Shannon diversity index of all crop types (SHDI). Additionally, we included the total area of patch and linear semi-natural habitats (SNH). These included for example unimproved grasslands, forests, hedges and grassy field boundaries. Landscape variables were not correlated across all regions (Table S3).

Arthropod traits

We selected four groups of traits that were expected to be influenced by local and landscape variables: body size, foraging type, dispersal capacity and reproduction type. All traits were compiled from available literature and databases. Butterfly traits were collected from (Bink 1992) and hoverflies traits from Syrph The Net database (Speight *et al.* 2015). Spider and carabid beetle traits were collected mainly from two databases: the Biological and Ecological functional Traits of Soil Invertebrates – BETSI (Hedde *et al.* 2012) and the carabids.org (Homburg *et al.* 2014) databases. Species traits missing from the databases were collected from further literature and from expert knowledge for spiders. These traits were added to the BETSI database. Trait categories or variables differed between taxa due to their different characteristics (Table 2). Body size was characterized by wing span for butterflies and body length for the other taxa. The foraging trait was characterized as foraging specialization for butterfly larvae, trophic position for carabid beetles and hoverfly larvae and hunting mode as well as preferred vertical stratum used by spiders. The dispersal trait was determined by gradients from low to high dispersal ability for flower-visitors and spiders whereas wing morphology was used for carabid beetles. Reproduction traits were classified into number of generations per year for flower-visitors and the breeding season for carabid beetles. For spiders, reproduction traits were not available and therefore not analysed in this study.

Statistical analysis

The link between arthropod abundance, traits and environmental variables was analysed with RLQ and partial RLQ using ade4 package in R (Dray & Dufour 2007). The analysis relates three tables: a environmental variable by site matrix (R-table), a species by site matrix (L-table) and a trait by species matrix (Q-table). Sites are here the sampled transects. The R-table included for each site local and landscape variables (Table 1) and the associated region. To avoid different weighting of regions due to different value ranges for landscape variables, we standardised these variables within each region. Values range between 0 and 1 as follows: $X_{range} = (X_{value} - X_{min}) / (X_{max} - X_{min})$ where X_{range} is the range value, X_{value} is the natural value, X_{min} and X_{max} are respectively the minimum and maximum value of the variables range. The L-table included species abundance summed over both visits and over traps within transects. Rare species occurring less than five times were excluded from the analysis. The number of sites analysed differed for each taxon. For hoverflies, we excluded transects if more than one of the six pan traps was lost. For butterflies and hoverflies, the whole field was excluded from analysis if one of the transects got lost across visits. For spiders and carabid beetles, we excluded the whole field if more than one of the four pitfall traps per visit was lost. The number of analysed sites was 1100 for butterflies in 291 landscapes, 446 for hoverflies in 392 landscapes, 568 for carabid beetles in 508 landscapes and 576 for spiders in 518 landscapes.

First, we analysed the three tables in separate ordinations. Principal component analysis was conducted on the R- and Q-table. We used the Hill and Smith method (Hill & Smith 1976) for mixed quantitative and categorical variables. The L-table underwent a correspondence analysis. The data was Hellinger transformed (Legendre & Gallagher 2001) to standardise species abundance.

Second, we performed a classical RLQ analysis of the three tables. The regions explained most the variance on the two first RLQ axes (for details see S4). As this study focuses on regional trends and not intra-regional ones, we performed a partial RLQ analysis. This analysis was used to control for the region by removing the variation that is linked to this factor (Wesuls *et al.* 2012). Pearson correlation was used to test the significance of species traits and environmental variables with the two first partial RLQ axes. Significant relations ($P < 0.05$) with a coefficient $|r| > 0.5$ were considered as strong correlations.

Finally, we tested for spatial autocorrelation in the variance unexplained by the RLQ axes using Moran's I test for each taxon (gearymoran function in ade4 package). We did not detect any signs of spatial autocorrelation after 999 randomization tests (Thioulouse *et al.* 1995; Gámez-Virués *et al.* 2015).

Results

Overall, our final data set contained 355 arthropod species (31 butterflies, 39 hoverflies, 90 carabids and 195 spiders) and 77,011 individuals (3,704 butterflies, 20,673 hoverflies, 23,504 carabids and 29,130 spiders) across all seven sampling regions (see species list and abundance in Table S5). For all four taxa the association of traits and environmental variables explained a high proportion of the co-inertia in the partial RLQ analysis (84.11-97.06%, Table 3). The position of each environmental and trait variable is shown in the partial RLQ biplot (Fig. 1). A summary of species scores on partial RLQ axes can be found in Table S5. We considered arthropod traits to be associated with certain environmental variables if both were highly and significantly correlated ($P < 0.05$) with one of the two first partial RLQ axes (Pearson $|r|>0.5$).

Local scale

We found across all arthropod taxa that local environmental variables were consistently and highly correlated with the first axis (Table 4) that accounted for most of the variation in the partial RLQ analysis (64.22-86.80%, Table 3). For all taxa this axis separated interior from border transect position and was also associated with flower cover for flower-visiting and plant species richness for ground-dwelling taxa (Fig. 1, Table 4). All four arthropod traits (body size, foraging and dispersal capacity and reproduction type) were influenced by these local variables as they were correlated with the first axis for different taxa (Table 5).

Based on high correlations with the first axis we found butterflies with smaller, but spiders with larger body sizes in the border transects. Foraging traits also showed high correlations with the first axis: Herbivorous carabid beetles (For.H), non-predatory hoverfly larvae (For.NPr) and hunting spiders (Hunt) were positively associated with border transects, whereas web building spiders (Web) responded negatively. Additionally, we found strong evidence that field borders enhance species with low dispersal capacity in three of the four taxa. Field borders were associated with non-migrating hoverflies (No.Mig), butterflies with low mobility (Disp) and spiders that do not balloon (No.bal). Reproduction traits were correlated with the first axis for flower-visiting taxa only. The number of generations per year increased from border to interior transects for butterflies, and also hoverfly species with a high number of generations (Gen>2) were negatively associated with border and positively with interior transects in the partial RLQ.

Landscape variables

For all taxa, landscape variables were correlated with the second axis that accounted for 10-20% of the co-inertia (Table 3). This axis was related to foraging and reproduction traits, but not body size and dispersal capacity. Different parts of crop heterogeneity played a role in shaping trait community composition for particular taxa as shown by their strong correlation with the second axis.

In landscapes with high crop compositional heterogeneity we found more spiders that search for their prey in the vegetation and the soil (Strat.SV) compared to those that hunt only on the soil (Stat.S), as well as more hoverflies with only one generation per year (Gen.1).

Higher configurational heterogeneity (more field borders, smaller fields) in the landscape influenced foraging and reproduction traits. There was a positive effect on oligophagous butterflies (For.O), whereas monophagous butterfly species (For.M) were negatively affected. Furthermore, predatory carabid beetles (For.Pr) responded positively and late breeding carabid species (Late.Br) negatively to high configurational crop heterogeneity.

The amount of semi-natural habitat in the landscape was correlated with the second axis across all taxa (Table 4). Based on this correlation and the arrow length in the RLQ biplot it was more important for shaping trait community composition than crop heterogeneity for butterflies and carabid beetles, but for hoverflies and spiders one of the crop heterogeneity components had an equal or even higher influence (Fig. 1, Table 4). Semi-natural habitats affected foraging and reproduction traits for different taxa, but not body size and dispersal capacity. Oligophagous butterflies (For.O), predatory carabid beetles (For.Pr) and spiders that search for their prey on the soil (Stat.S) showed a positive association with increasing amounts of semi-natural habitats. However, monophagous butterflies were negatively affected (For.M). Additionally, hoverflies with only one generation per year (Gen.1) were positively and late breeding carabid beetles (Late.Br) negatively correlated with semi-natural habitats.

Table 1 Description of environmental variables used in partial RLQ and their abbreviations (Abb.). Landscape parameters were calculated within 1 km² (1×1 km square).

Environmental variables	Abb.	Range	Mean ± Std. dev.
Local parameters			
Field border transect	Border		
Field interior transect	Interior		
Flower cover around pan traps* (%)	Flower	0.0 - 52.8	2.4 ± 5.0
Flower cover inside transect** (%)	Flower	0.0 - 44.0	1.7 ± 4.1
Weed species richness inside transect	Plant	0.0 - 64.0	12.2 ± 9.7
Landscape parameters			
Crop Shannon diversity	SHDI	0 - 2.0	1.0 ± 0.4
Total field border length per crop area ($km.ha^{-1}$)	TBL	0.7 - 6.5	2.6 ± 1.0
Semi-natural habitat area cover (%)	SNH	0.2 - 38.6	12.6 ± 7.7

* for hoverflies; ** for butterflies

Table 2 Functional traits of the four taxa used for partial RLQ and their abbreviations. All traits are categorical apart of those marked with a star (*).

Traits	Variable	Abb.
Butterfly		
Body size	Wing span* (mm)	BS
Foraging	Polyphagous	For.P
	Oligophagous	For.O
	Monophagous	For.M
Dispersal	Form low (0) to high (6) dispersal ability*	Disp
Reproduction	Number of generation per year* (1 to 4)	Gen
Hoverfly		
Body size	Body length* (mm)	BS
Foraging	Predator	For.PR
	Non predator	For.NPr
Dispersal	No migration	No.Mig
	Weak migration	W.Mig
	Strong migration	S.Mig
Reproduction	1 generation per year	Gen1
	2 generations per year	Gen2
	More than 2 generations per year	Gen>2
Carabid beetle		
Body size	Body length* (mm)	BS
Foraging	Predatory	For.Pr
	Omnivorous	For.O
	Herbivorous	Hor.H
Dispersal	Short winged (Short.W)	Short.W
	Wing dimorphic (Dim.W)	Dim.W
	Fully winged	Wing
Reproduction	Early breeder (spring)	Ear.Br
	Late breeder (summer/ autumn/ winter)	Late.Br
	Both early and late breeder	EL.Br
Spiders		
Body size	Body length* (mm)	BS
Foraging	Soil dwelling	Strat.S
	Soil and vegetation dwelling	Strat.SV
	Vegetation dwelling	Strat.V
	Hunting	Hunt
	Web builder	Web
Dispersal	No ballooning	No.Bal
	Uncommon ballooning	Un.Bal
	Ballooning	Bal

Table 3 Results of the partial RLQ analysis for the first two axes.

	Eigenvalue		Projected Inertia %	
	Axis 1	Axis 2	Axis 1	Axis 2
Butterfly	0.046	0.010	77.657	17.443
Hoverfly	0.025	0.003	84.101	11.031
Carabid beetle	0.016	0.005	64.219	19.892
Spider	0.052	0.006	86.800	10.263

Table 4 Pearson correlation between environmental variables and partial RLQ axes. Significant correlations with pearson |r| > 0.5 are in bold characters.

	Butterfly		Syrphidae		Carabids		Spiders	
Environmental variables	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Local parameters								
Border	**0.91****	-0.14**	**0.80****	0.02	**0.91****	0.15**	**0.98****	0.11***
Interior	**-0.91****	0.14**	**-0.80****	-0.02	**-0.91****	-0.15**	**-0.98****	-0.11***
Flower	**0.57****	-0.26**	**0.81****	0.05				
Plant					**0.63****	-0.004	**0.52****	-0.04
Landscape parameters								
SHDI	-0.09**	0.17**	-0.11**	**0.78****	0.11**	0.44**	0.10**	**-0.65*****
TBL	0.10**	**0.65****	0.14**	0.17**	-0.18**	**0.60****	0.06	0.22***
SNH	0.24**	**0.74****	0.17**	**0.58****	-0.17**	**0.76****	-0.06*	**0.65*****

* P-value < 0.05

Table 5 Pearson correlation between environmental variables and partial RLQ axes. Significant correlations with pearson |r| > 0.5 are in bold characters.

Traits	Axis 1	Axis 2
Butterfly		
Wing span (mm)	**-0.80 ****	0.40 *
Polyphagous	-0.23	0.02
Oligophagous	0.46 **	**0.56 ****
Monophagous	-0.30	**-0.78 ****
Form low (0) to high (6) dispersal ability	**-0.89 ****	-0.10
Number of generation per year (1 to 4)	**-0.64 ****	**-0.56 ****
Hoverfly		
Body length (mm)	0.45 **	0.05
Predator	**-0.83 ****	0.13
Non predator	**0.83 ****	-0.13
No migration	**0.63 ****	0.38 *
Weak migration	-0.27	-0.29
Strong migration	-0.49 **	-0.19
1 generation per year	0.27	**0.86 ****
2 generations per year	0.49 **	**-0.69 ****
More than 2 generations per year	**-0.68 ****	< -0.00
Carabid beetle		
Body length (mm)	0.03	-0.37 **
Predatory	-0.46 **	**0.75 ****
Omnivorous	-0.46 **	-0.44 **
Herbivorous	**0.94 ****	-0.49 **
Short winged	0.10	0.14
Wing dimorphic	-0.21 *	0.31 **
Fully winged	0.14	-0.37 **
Early breeder (spring)	0.08	0.42 **
Late breeder (summer/ autumn/ winter)	-0.003	**-0.59 ****
Both early and late breeder	-0.15	0.27 *
Spiders		
Body length (mm)	**0.70 ****	-0.09
Soil dwelling	0.22 **	**0.96 ****
Soil and vegetation dwelling	-0.28 **	**-0.84 ****
Vegetation dwelling	0.14	-0.40 **
Hunting	**0.82 ****	-0.11
Web builder	**-0.82 ****	0.11
No ballooning	**0.66 ****	0.11
Uncommon ballooning	0.08	-0.20 **
Ballooning	**-0.69 ****	-0.03

* 0.05 > P-value > 0.01; ** P-value < 0.01

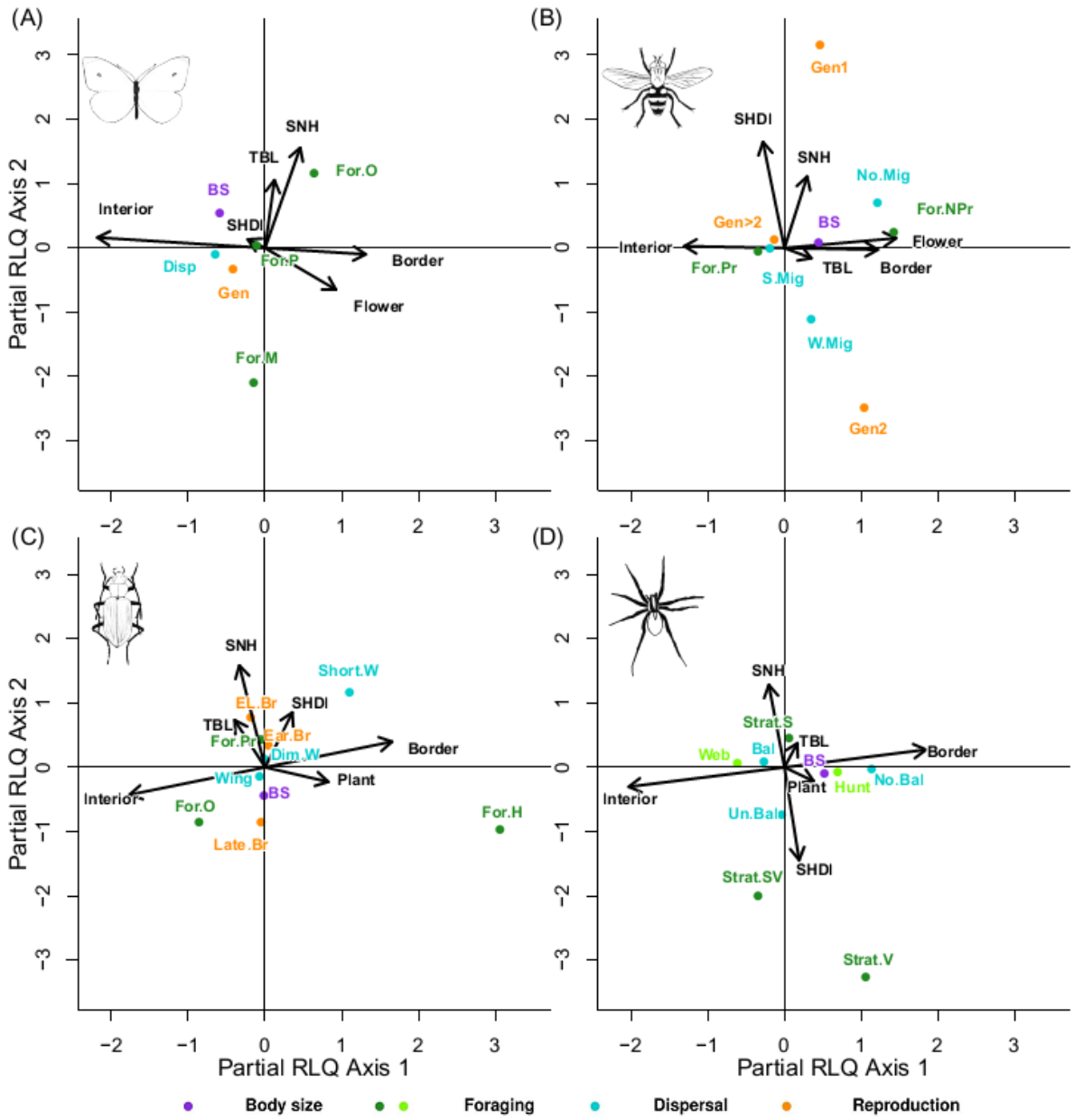


Figure 1 Partial RLQ ordination of environmental variables (arrows) and traits for butterflies (A), hoverflies (B), carabid beetles (C) and spiders (D). Differently coloured dots represent traits for reproduction (orange), dispersal (blue), foraging (green) and body size (purple). For illustration purpose, environmental variable scores have been upscaled. Abbreviations are detailed in table 2 for trait levels and in table 1 for environmental variables.

Discussion

Our study provides novel evidence that landscape heterogeneity as determined by the crop production area is shaping the community trait composition of flower-visiting and ground-dwelling arthropods in agricultural landscapes. Crop configurational heterogeneity promoted butterflies and carabid beetles with high feeding specialization, while high crop compositional heterogeneity supported hoverflies with low reproduction potential and habitat generalist among the spiders. However, these landscape variables played only a minor role compared to local proximity of field margins that was the most important factor structuring the trait composition of arthropods communities in cereal fields.

Local scale

Field location (border vs. interior) was a consistent driver for trait composition across all taxa. Field margins in agricultural landscapes provide food resources and shelter from within-field disturbance, which benefits species richness of many arthropods (Bianchi *et al.* 2006; Marshall *et al.* 2006; Öckinger & Smith 2007; Vickery *et al.* 2009). Therefore, the proximity to semi-natural field margins with their higher cover of plants and flowering resources was probably responsible for the strong impact of local field position on arthropod traits.

First of all, we found strong evidence that body size and dispersal traits, which are usually highly correlated (Greenleaf *et al.* 2007), strongly differ between field borders and interiors for most taxa. In field borders we found smaller and less mobile butterflies, non-migrating hoverflies and larger, but non-ballooning spiders. Dispersal capacity is an important trait, because it facilitates (re)-colonization of distant habitats and gene flow between populations (Lester *et al.* 2007). Only highly mobile species used field interiors, whereas species with lower dispersal capacity were restricted to field borders indicating their importance as corridors in agro-ecosystems. However, characteristics of species with high dispersal ability can greatly differ between taxa. For spiders small and light species are usually ballooning such as Linyphiidae (Bell *et al.* 2005) and thus more mobile than large and heavy species that live on the ground (e.g. Lycosidae). On the contrary, larger butterflies species are usually better dispersers (Öckinger *et al.* 2010) explaining why field borders promoted larger spider, but smaller butterfly species.
The second trait influenced by local field position was foraging, as field borders promoted non-predatory carabid beetle and hoverfly species. This suggests that high weed diversity in field borders is essential for herbivorous arthropod species that are usually confined to more semi-natural habitats to find their food resources (Frank 1999; Haenke *et al.* 2009; Birkhofer *et al.* 2014). This is important, as more phytophagous carabid species mean enhanced seed predation (Bohan *et al.* 2011), contributing to weed seed predation in crops (Jonason *et al.* 2013). On the contrary, cereal field interiors provide higher food resource availability for predatory arthropods, e.g. due to higher densities of pest species like aphids (Caballero-López *et al.* 2012). All predatory hoverflies (at larval stage) were aphidophagous in our study and many carabid species feed on aphids (Bell *et al.* 2008), explaining their association with field interiors. Additionally, hunting spiders preferred border transects in contrast to those that build webs, probably because these species usually also have low dispersal capacity.

Local field border position influenced also reproduction traits of flower-visitors. The field interior filtered for butterfly and hoverfly species with a high number of generations per year. This is in line with other studies showing that high and fast reproducing butterflies are favoured in arable land (Hanspach *et al.* 2015) or in more intensively managed grasslands (Börschig *et al.* 2013). Thus, the results confirm our hypothesis that species with a low reproduction potential strongly depend on resources provided by semi-natural field boundaries to persist in agricultural landscapes.

Landscape scale

Landscape variables played a role for only foraging and reproduction traits, with different landscape variables being important for different sets of taxa. This is in contrast to the local scale that affected all arthropod traits included in our analyses.

Higher crop compositional heterogeneity at the landscape scale favoured generalist spiders that search for their prey in the vegetation, but also on the soil and hoverflies with only one generation per year. The beneficial effect of crop diversity on spider species using both, the soil and the vegetation layer, can be explained by a higher availability of niche-space (Díaz *et al.* 2013) in diverse landscapes. The availability of several crop types with different vegetation structures and management may benefit species which can switch between niches. Additionally, these differences between crops can lead to complementary weed communities (Hyvönen & Salonen 2002) possibly resulting in higher diversity of flowering resources throughout the season. This might be the reason why hoverfly species with only one generation could also benefit from higher crop diversity, as species with low reproductive potential are especially dependent on high resource provision (Henle *et al.* 2004).

However, we did not find more predatory communities in landscapes with low crop compositional heterogeneity as expected in our hypothesis. We assumed that more pest species would be available in landscapes dominated by monocultures (Veres *et al.* 2013), but pesticide applications in conventionally managed fields probably avoided large pest outbreaks that could be responsible for major shifts to predatory communities. Additionally, we could not confirm that crop diversity has similar universal positive effects on arthropod feeding specialists as compositional diversity of semi-natural habitat (Gámez-Virués *et al.* 2015).

We provide novel evidence that crop configurational heterogeneity can mitigate the fragmentation effects of agricultural production areas on butterflies and carabids with higher feeding specialization. Oligophagous butterfly species preferred landscapes with smaller fields, whereas the non-specialized polyphagous species were not affected by landscape variables.

Similar to butterflies, crop configuration affected foraging traits of carabid beetles and filtered for more predatory species supporting the hypothesis that higher trophic level species are more sensitive to land use change (Tscharntke & Brandl 2004). Higher crop configuration provides more opportunities for spill-over between habitat patches, since higher field interspersion lowers the distances between patches and thus increases connectivity between habitats (Fahrig *et al.* 2011). Additionally, linear elements in agricultural landscapes can support insect movements (Van Geert *et al.* 2010; Cranmer *et al.* 2012), possibly resulting in a higher connectedness of food resources supporting feeding specialists (Öckinger *et al.* 2010).

The negative impact of configurational heterogeneity on monophagous species was unexpected. We expected monophages to benefit from higher configuration. Though, in our study these species were mostly feeding on widespread plants in cultivated landscapes (Rand & Tscharntke 2007), e.g. nettle (*Urtica dioica*) or field pansy (*Viola arvensis*), explaining their association with large field sizes. Additionally, we could not confirm the hypothesis that landscapes with a high density of field borders would affect dispersal traits (Perović *et al.* 2015). This indicates that crop borders are less important for dispersal in different arthropod groups compared to borders between other habitat types (Gámez-Virués *et al.* 2015).

Semi-natural habitats affected foraging and reproduction traits, but not dispersal and body size. However, all arthropod taxa were affected by semi-natural areas. First of all, semi-natural habitat filtered for more specialized feeders in butterflies and carabids, similar to crop configuration. Plant species richness in these diverse habitat types probably benefitted oligophagous butterflies (van Swaay 2002; Billeter *et al.* 2008), whereas monophagous butterflies that are specialized on common agricultural weeds could profit from higher crop cover. Secondly, the high flower resource provision in semi-natural habitats probably also supported hoverfly species with low reproductive potential (Henle *et al.* 2004). Additionally, predatory carabids were promoted by high semi-natural cover, but this relation may be better explained by the reproduction strategies of these species. Predatory carabids were as well breeding in spring and generally overwintering in non-crop habitats (Purtauf *et al.* 2005), in contrast to the species breeding later, which were rather associated to landscapes with more crop cover where some of them overwinter (Purtauf *et al.* 2005). Finally, soil dwelling spiders could possibly profit from less disturbed soil in semi-natural habitats and field margins (Birkhofer *et al.* 2015). These results highlight the vital importance of non-crop habitats in agricultural landscapes for functionally diverse arthropod communities (Tscharntke *et al.* 2008; Öckinger *et al.* 2010).

Conclusions

In conclusion, our study shows a consistent trend for all flower-visiting and predatory arthropod taxa that trait community composition shifts strongly from field borders to interiors by filtering for generalist species with high dispersal capacity and predatory feeding requirements. At the landscape level, semi-natural habitat presence selected consistently lower reproductive species for flower-visitors and more specialised foraging traits for biocontrol agents. Therefore, our results reinforce the importance of semi-natural area in agricultural landscapes including field margins to conserve more specialised species traits, supporting the landscape-moderated functional trait selection hypothesis (Tscharntke *et al.* 2012).

Nevertheless, we demonstrate for the first time that changes in landscape scale crop configuration and composition alter trait composition of arthropods as well, even if the effects were more disparate between taxa. A homogenisation of landscapes as defined by (Gámez-Virués *et al.* 2015) includes loss of spatial configuration and habitat diversity and benefits arthropods with more generalist traits. Likewise, in our study the cereal-field arthropod communities with low reproductive or specialised feeders were favoured in landscapes with smaller fields (butterflies and carabid beetles) or landscapes with higher crop diversity (hoverflies). This is important since functional traits of flower-visiting and ground-dwelling arthropods are likely to have consequences on ecosystem services such as pollination (Fründ *et al.* 2013; Lavorel *et al.* 2013) and biological pest control (Rusch *et al.* 2015). Thus, we recommend that in future landscape management strategies encourage reduction in crop field size and crop diversification.

Acknowledgements

This study was part of the FarmLand project funded by the ERA-Net BiodivERsA (http://farmland-biodiversity.org). Specific national funders were: French National Research Agency (ANR-11-EBID-0004), German Federal Ministry of Education and Research (BMBF) and Spanish Ministry of Economy and Competitiveness, part of the 2011 BiodivERsA call for research proposals. The funding scheme for UK was the UK Government Department of the Environment, Food and Rural Affairs (Defra, project WC1034). The author A.B.B. was supported by a scholarship from the German Academic Exchange Service (DAAD).

We thank all farmers who allowed us to sample on their fields, and the many fieldwork-helpers. A special thank goes to Yvan Capowiez and Alain Pasquet for providing further expert knowledge and help with spider traits. We are especially thankful to David Perović for help on statistical analysis and constructive comments on an earlier version of the manuscript and to Stéphane Dray for statistical advice.

References

1.
Bell, J.R., Bohan, D.A., Shaw, E.M. & Weyman, G.S. (2005). Ballooning dispersal using silk: world fauna, phylogenies, genetics and models. *Bull. Entomol. Res.*, 95, 69–114.

2.
Bell, J.R., Mead, A., Skirvin, D.J., Sunderland, K.D., Fenlon, J.S. & Symondson, W.O.C. (2008). Do functional traits improve prediction of predation rates for a disparate group of aphid predators? *Bull. Entomol. Res.*, 98, 587.

3.
Bianchi, F.J.J.., Booij, C.J.. & Tscharntke, T. (2006). Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. *Proc. R. Soc. B Biol. Sci.*, 273, 1715–1727.

4.
Billeter, R., Liira, J., Bailey, D., Bugter, R., Arens, P., Augenstein, I., *et al.* (2008). Indicators for biodiversity in agricultural landscapes: a pan-European study: Biodiversity in European Agro-ecosystems. *J. Appl. Ecol.*, 45, 141–150.

5.
Bink, F.A. (1992). *Ecologische atlas van de dagvlinders van Noordwest-Europa*. Schuyt & Co Uitgevers en Importeurs, Haarlem.

6.
Birkhofer, K., Smith, H.G., Weisser, W.W., Wolters, V. & Gossner, M.M. (2015). Land-use effects on the functional distinctness of arthropod communities. *Ecography*, 38, 889–900.

7.
Birkhofer, K., Wolters, V. & Diekötter, T. (2014). Grassy margins along organically managed cereal fields foster trait diversity and taxonomic distinctness of arthropod communities. *Insect Conserv. Divers.*, 7, 274–287.

8.
Blitzer, E.J., Dormann, C.F., Holzschuh, A., Klein, A.-M., Rand, T.A. & Tscharntke, T. (2012). Spillover of functionally important organisms between managed and natural habitats. *Agric. Ecosyst. Environ.*, 146, 34–43.

9.
Bohan, D.A., Boursault, A., Brooks, D.R. & Petit, S. (2011). National-scale regulation of the weed seedbank by carabid predators: Carabid seed predation. *J. Appl. Ecol.*, 48, 888–898.

10.
Bommarco, R., Biesmeijer, J.C., Meyer, B., Potts, S.G., Poyry, J., Roberts, S.P.M., *et al.* (2010). Dispersal capacity and diet breadth modify the response of wild bees to habitat loss. *Proc. R. Soc. B Biol. Sci.*, 277, 2075–2082.

11.
Börschig, C., Klein, A.-M., von Wehrden, H. & Krauss, J. (2013). Traits of butterfly communities change from specialist to generalist characteristics with increasing land-use intensity. *Basic Appl. Ecol.*, 14, 547–554.

12.
Caballero-López, B., Bommarco, R., Blanco-Moreno, J.M., Sans, F.X., Pujade-Villar, J., Rundlöf, M., *et al.* (2012). Aphids and their natural enemies are differently affected by habitat features at local and landscape scales. *Biol. Control*, 63, 222–229.

13.
Cosentino, B.J., Schooley, R.L. & Phillips, C.A. (2011). Connectivity of agroecosystems: dispersal costs can vary among crops. *Landsc. Ecol.*, 26, 371–379.

14.
Cranmer, L., McCollin, D. & Ollerton, J. (2012). Landscape structure influences pollinator movements and directly affects plant reproductive success. *Oikos*, 121, 562–568.

15.
Díaz, S., Purvis, A., Cornelissen, J.H.C., Mace, G.M., Donoghue, M.J., Ewers, R.M., *et al.* (2013). Functional traits, the phylogeny of function, and ecosystem service vulnerability. *Ecol. Evol.*, 3, 2958–2975.

16.
Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B. & Collen, B. (2014). Defaunation in the Anthropocene. *Science*, 345, 401–406.

17.
Dray, S. & Dufour, A.-B. (2007). The ade4 Package: Implementing the Duality Diagram for Ecologists. *J. Stat. Softw.*, 22.

18.
Duflot, R., Georges, R., Ernoult, A., Aviron, S. & Burel, F. (2014). Landscape heterogeneity as an ecological filter of species traits. *Acta Oecologica*, 56, 19–26.

19.
Fahrig, L., Baudry, J., Brotons, L., Burel, F.G., Crist, T.O., Fuller, R.J., *et al.* (2011). Functional landscape heterogeneity and animal biodiversity in agricultural landscapes: Heterogeneity and biodiversity. *Ecol. Lett.*, 14, 101–112.

20.
Frank, T. (1999). Density of adult hoverflies (Dipt., Syrphidae) in sown weed strips and adjacent fields. *J. Appl. Entomol.*, 123, 351–355.

21.
Fründ, J., Dormann, C.F., Holzschuh, A. & Tscharntke, T. (2013). Bee diversity effects on pollination depend on functional complementarity and niche shifts. *Ecology*, 94, 2042–2054.

22.
Gámez-Virués, S., Perović, D.J., Gossner, M.M., Börschig, C., Blüthgen, N., de Jong, H., *et al.* (2015). Landscape simplification filters species traits and drives biotic homogenization. *Nat. Commun.*, 6, 8568.

23.
Garibaldi, L.A., Steffan-Dewenter, I., Kremen, C., Morales, J.M., Bommarco, R., Cunningham, S.A., *et al.* (2011). Stability of pollination services decreases with isolation from natural areas despite honey bee visits: Habitat isolation and pollination stability. *Ecol. Lett.*, 14, 1062–1072.

24.
Greenleaf, S.S., Williams, N.M., Winfree, R. & Kremen, C. (2007). Bee foraging ranges and their relationship to body size. *Oecologia*, 153, 589–596.

25.
Haenke, S., Scheid, B., Schaefer, M., Tscharntke, T. & Thies, C. (2009). Increasing syrphid fly diversity and density in sown flower strips within simple vs. complex landscapes. *J. Appl. Ecol.*, 46, 1106–1114.

26.
Hanspach, J., Loos, J., Dorresteijn, I., von Wehrden, H., Moga, C.I. & David, A. (2015). Functional diversity and

trait composition of butterfly and bird communities in farmlands of Central Romania. *Ecosyst. Health Sustain.*, 1, 1–8.

27.
Hedde, M., Pey, B., Auclerc, A., Capowiez, Y., Cluzeau, D., Cortet, J., Decaëns, T., Deharveng, L., Dubs, F., Joimel, S., Guernion, M., Grumiaux, F., Laporte, M.-A., Nahmani, J., Pasquet, A., Pelosi, C., Pernin, C., Ponge, J.-F., Salmon, S. & Santorufo, L. (2012) BETSI, a complete framework for studying soil invertebrate functional traits. XVI ICSZ—International Colloquium on Soil Zoology, Coimbra

28.
Hendrickx, F., Maelfait, J.-P., Desender, K., Aviron, S., Bailey, D., Diekotter, T., *et al.* (2009). Pervasive effects of dispersal limitation on within- and among-community species richness in agricultural landscapes. *Glob. Ecol. Biogeogr.*, 18, 607–616.

29.
Hendrickx, F., Maelfait, J.-P., Van Wingerden, W., Schweiger, O., Speelmans, M., Aviron, S., *et al.* (2007). How landscape structure, land-use intensity and habitat diversity affect components of total arthropod diversity in agricultural landscapes. *J. Appl. Ecol.*, 44, 340–351.

30.
Henle, K., Davies, K.F., Kleyer, M., Margules, C. & Settele, J. (2004). Predictors of Species Sensitivity to Fragmentation. *Biodivers. Conserv.*, 13, 207–251.

31.
Hill, M.O. & Smith, A.J.E. (1976). Principal Component Analysis of Taxonomic Data with Multi-State Discrete Characters. *Taxon*, 25, 249.

32.
Homburg, K., Homburg, N., Schäfer, F., Schuldt, A. & Assmann, T. (2014). Carabids.org - a dynamic online database of ground beetle species traits (Coleoptera, Carabidae). *Insect Conserv. Divers.*, 7, 195–205.

33.
Hyvönen, T. & Salonen, J. (2002). Weed species diversity and community composition in cropping practices at two intensity levels – a six-year experiment. *Plant Ecol.*, 159, 73–81.

34.
Jonason, D., Smith, H.G., Bengtsson, J. & Birkhofer, K. (2013). Landscape simplification promotes weed seed predation by carabid beetles (Coleoptera: Carabidae). *Landsc. Ecol.*, 28, 487–494.

35.
Klein, A.-M., Vaissiere, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., *et al.* (2007). Importance of pollinators in changing landscapes for world crops. *Proc. R. Soc. B Biol. Sci.*, 274, 303–313.

36.
Lavorel, S., Storkey, J., Bardgett, R.D., de Bello, F., Berg, M.P., Le Roux, X., *et al.* (2013). A novel framework for linking functional diversity of plants with other trophic levels for the quantification of ecosystem services. *J. Veg. Sci.*, 24, 942–948.

37.
Legendre, P. & Gallagher, E. (2001). Ecologically meaningful transformations for ordination of species data. *Oecologia*, 129, 271–280.

38.
Lester, S.E., Ruttenberg, B.I., Gaines, S.D. & Kinlan, B.P. (2007). The relationship between dispersal ability and geographic range size. *Ecol. Lett.*, 10, 745–758.

39.
Marshall, E.J.P., West, T.M. & Kleijn, D. (2006). Impacts of an agri-environment field margin prescription on the flora and fauna of arable farmland in different landscapes. *Agric. Ecosyst. Environ.*, 113, 36–44.

40.
Newbold, T., Hudson, L.N., Hill, S.L.L., Contu, S., Lysenko, I., Senior, R.A., *et al.* (2015). Global effects of land use on local terrestrial biodiversity. *Nature*, 520, 45–50.

41.
Öckinger, E., Schweiger, O., Crist, T.O., Debinski, D.M., Krauss, J., Kuussaari, M., *et al.* (2010). Life-history traits predict species responses to habitat area and isolation: a cross-continental synthesis: Habitat fragmentation and life-history traits. *Ecol. Lett.*, no–no.

42.
Öckinger, E. & Smith, H.G. (2007). Semi-natural grasslands as population sources for pollinating insects in agricultural landscapes: Population sources for pollinators. *J. Appl. Ecol.*, 44, 50–59.

43.
Palmu, E., Ekroos, J., Hanson, H.I., Smith, H.G. & Hedlund, K. (2014). Landscape-scale crop diversity interacts with local management to determine ground beetle diversity. *Basic Appl. Ecol.*, 15, 241–249.

44.
Perović, D., Gámez-Virués, S., Börschig, C., Klein, A.-M., Krauss, J., Steckel, J., *et al.* (2015). Configurational landscape heterogeneity shapes functional community composition of grassland butterflies. *J. Appl. Ecol.*, 52, 505–513.

45.
Prugh, L.R., Hodges, K.E., Sinclair, A.R.E. & Brashares, J.S. (2008). Effect of habitat area and isolation on fragmented animal populations. *Proc. Natl. Acad. Sci.*, 105, 20770–20775.

46.
Purtauf, T., Roschewitz, I., Dauber, J., Thies, C., Tscharntke, T. & Wolters, V. (2005). Landscape context of organic and conventional farms: Influences on carabid beetle diversity. *Agric. Ecosyst. Environ.*, 108, 165–174.

47.
Rand, T.A. & Tscharntke, T. (2007). Contrasting effects of natural habitat loss on generalist and specialist aphid natural enemies. *Oikos*, 116, 1353–1362.

48.
Rusch, A., Birkhofer, K., Bommarco, R., Smith, H.G. & Ekbom, B. (2015). Predator body sizes and habitat preferences predict predation rates in an agroecosystem. *Basic Appl. Ecol.*, 16, 250–259.

49
Speight, M.C.D., Castella, E., Sarthou, J.-P. & Vanappelghem, C. (2015) Syrph the Net: The Database of European Syrphidae. Syrph the Net publications, Dublin.
50.
Steffan-Dewenter, I. & Tscharntke, T. (2000). Butterfly community structure in fragmented habitats. *Ecol. Lett.*, 3, 449–456.

51.
van Swaay, C.A.. (2002). The importance of calcareous grasslands for butterflies in Europe. *Biol. Conserv.*, 104, 315–318.

52.
Thioulouse, J., Chessel, D. & Champely, S. (1995). Multivariate analysis of spatial patterns: a unified approach to local and global structures. *Environ. Ecol. Stat.*, 2, 1–14.

53.
Tscharntke, T., Bommarco, R., Clough, Y., Crist, T.O., Kleijn, D., Rand, T.A., *et al.* (2007). Conservation biological control and enemy diversity on a landscape scale. *Biol. Control*, 43, 294–309.

54.
Tscharntke, T. & Brandl, R. (2004). Plant-insect interactions in fragmented landscapes. *Annu. Rev. Entomol.*, 49, 405–430.

55.
Tscharntke, T., Sekercioglu, C.H., Dietsch, T.V., Sodhi, N.S., Hoehn, P. & Tylianakis, J.M. (2008). Landscape constraints on functional diversity of birds and insects in tropical agroecosystems. *Ecology*, 89, 944–951.

56.
Tscharntke, T., Tylianakis, J.M., Rand, T.A., Didham, R.K., Fahrig, L., Batáry, P., *et al.* (2012). Landscape moderation of biodiversity patterns and processes - eight hypotheses. *Biol. Rev.*, 87, 661–685.

57.
Van Geert, A., Van Rossum, F. & Triest, L. (2010). Do linear landscape elements in farmland act as biological corridors for pollen dispersal?: Linear landscape elements as corridors. *J. Ecol.*, 98, 178–187.

58.
Veres, A., Petit, S., Conord, C. & Lavigne, C. (2013). Does landscape composition affect pest abundance and their control by natural enemies? A review. *Agric. Ecosyst. Environ.*, 166, 110–117.

59.
Vickery, J.A., Feber, R.E. & Fuller, R.J. (2009). Arable field margins managed for biodiversity conservation: A review of food resource provision for farmland birds. *Agric. Ecosyst. Environ.*, 133, 1–13.

60.
Watling, J.I., Nowakowski, A.J., Donnelly, M.A. & Orrock, J.L. (2011). Meta-analysis reveals the importance of matrix composition for animals in fragmented habitat: Connectivity meta-analysis. *Glob. Ecol. Biogeogr.*, 20, 209–217.

61.
Wesuls, D., Oldeland, J. & Dray, S. (2012). Disentangling plant trait responses to livestock grazing from spatio-temporal variation: the partial RLQ approach. *J. Veg. Sci.*, 23, 98–113.

Supplementary material

Fig. S1: Location of the seven sampled regions across Western Europe.

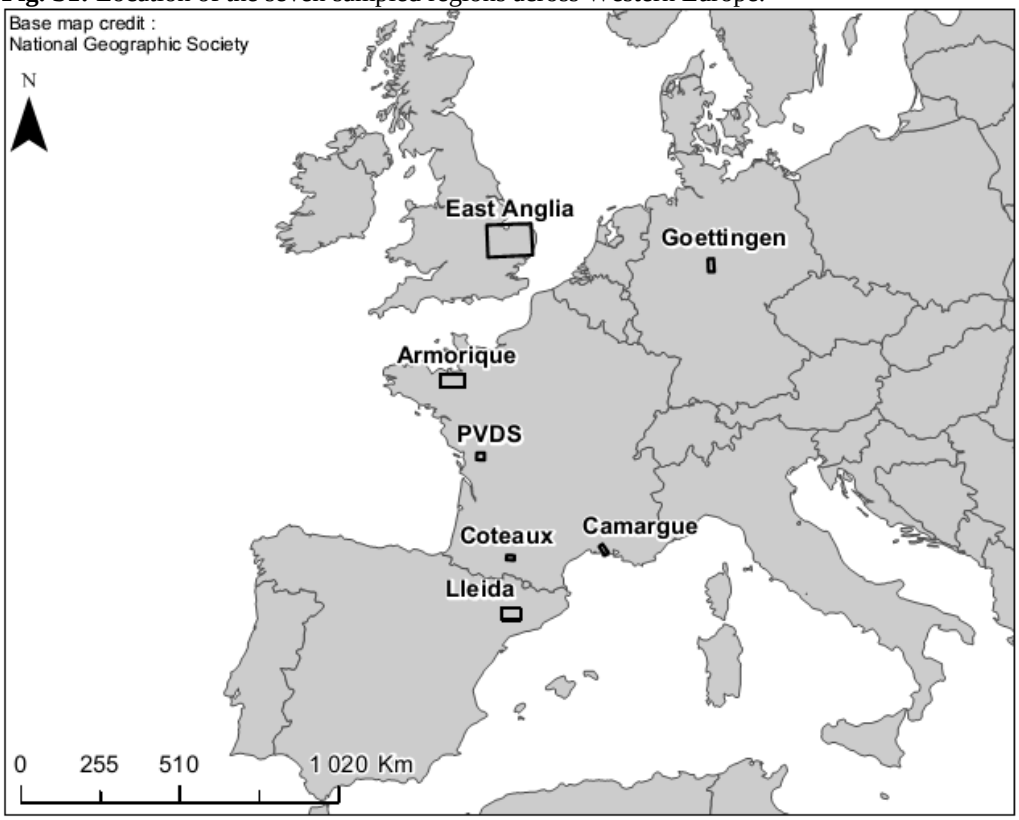


Fig. S2: Arthropods were sampled along two 50 m transects in the border and the interior of each field. Carabid beetles and spiders were sampled using pitfall traps, hoverflies with pan traps in different colours and butterflies were recorded with transect walks.

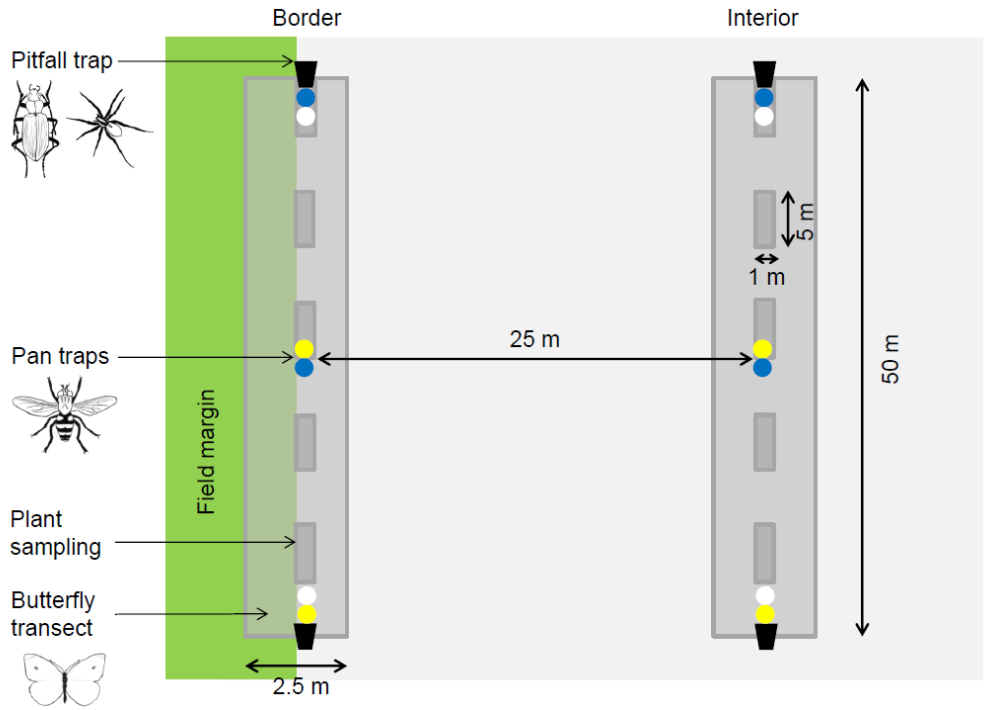


Table S3 Correlation between variables in the seven regions and across all regions. The range of correlation coefficient between the four taxa are shown. Correlations are generally low, apart from the positive relation between TBL and SNH in the region Coteaux (coefficient in bold). For the meaning of abbreviations, see Table 1 in the main text. The variables Flower/ plants is the flower cover for flower-visitors and plant species richness for carabid beetles and spiders.

	Pearson correlation coefficient r			
Variables	SHDI	TBL	SNH	Flower/ plants
All regions				
SHDI	1			
TBL	0.14 - 0.20	1		
SNH	-0.04 - 0.03	0.25 - 0.34	1	
Flower/ plants	0.01 - 0.08	-0.02 - 0.01	-0.03 - 0.04	1
Armorique				
SHDI	1			
TBL	-0.2 - -0.02	1		
semi	0.12 - 0.19	0.28 - 0.31	1	
Flower/ plants	-0.09 - 0.42	-0.16 - 0.02	-0.25 - -0.02	1
Camargue				
SHDI	1			
TBL	0.17-0.22	1		
SNH	-0.01- 0.06	0.25- 0.38	1	
Flower/ plants	-0.09- 0.08	-0.09- 0.08	0.03- 0.28	1
Coteaux				
SHDI	1			
TBL	-0.03- 0.16	1		
SNH	-0.03- -0.01	**0.50- 0.52**	1	
Flower/ plants	-0.21- 0.12	-0.07- 0.06	-0.19- 0.10	1
East-Anglia				
SHDI	1			
TBL	0.37- 0.48	1		
SNH	0.24- 0.29	0.14- 0.22	1	
Flower/ plants	-0.06- 0.08	0.00- 0.04	0.01- 0.15	1
Goettingen				
SHDI	1			
TBL	0.17- 0.18	1		
SNH	0.09- 0.09	0.04- 0.05	1	
Flower/ plants	0.08- 0.12	-0.04- 0.02	-0.03- 0.18	1
Lleida				
SHDI	1			
TBL	0.26- 0.28	1		
SNH	-0.22- -0.17	0.29- 0.33	1	
Flower/ plants	0.09- 0.21	-0.11- -0.05	0.02- 0.11	1

Table S3 (continued)

	SHDI	TBL	SNH	Flower/ plants
PVDS				
SHDI	1			
TBL	0.10- 0.17	1		
SNH	-0.03- 0.04	0.11- 0.43	1	
Flower/ plants	-0.09- -0.05	-0.10- -0.02	-0.10- -0.02	1

Supplement S4. RLQ analysis, relating environmental variables and regions to species traits of the four taxa.
The first axes of the classical RLQ explained between 79 and 92% of the variance in butterflies, hoverflies, carabid beetles and spiders (Table 1). Among all variables, the regions were the most important one structuring communities of the four taxa (Fig. 1)

Table 1 Results of the classical RLQ analysis for the first two axes.

	Eigenvalue		Projected Inertia %		Cum. Inertia %	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Butterfly	0.37	0.15	61.49	24.04	61.49	85.53
Hoverfly	0.42	0.13	70.67	21.63	70.67	92.29
Carabid beetle	0.13	0.1	45.91	32.94	45.91	78.85
Spider	0.17	0.06	64.67	25.30	64.67	89.97

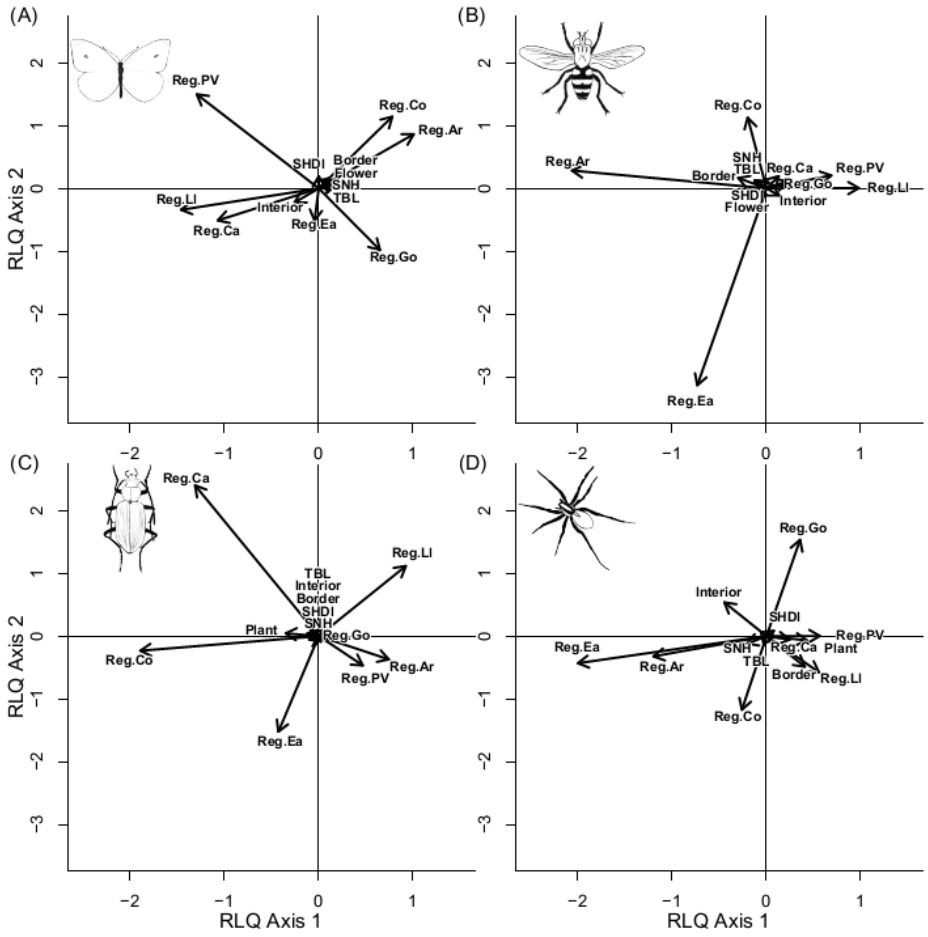


Fig. 1 Illustration of the importance the regions for the structure of butterfly (A), hoverfly (B), carabid beetles (C) and spider (D) communities. Biplots represent RLQ ordination of environmental variables. Reg.Ar= Armorique region, Reg.CA= Camargue region, Reg.CO= Coteaux region, Reg.EA= East-Anglia region, Reg.Go= Goettingen region and Reg.PV= PVDS region. For abbreviations meaning of the other variables, see Table 1 in the main text.

CHAPTER 3
Biological pest control across Europe depend on cascading effects of landscape crop heterogeneity and species traits

Article in preparation

Aliette Bosem Baillod, Teja Tscharntke, Péter Batáry, Colette Bertand, Nicolas Gross, Annika Hass, Clélia Sirami, Jean-Louis Martin, Lenore Fahrig, Cyrille Violle, José Antonio Barrientos, Alexis Saintilan, Jacques Baudry, Gerard Bota, Vincent Bretagnolle, Lluis Brotons, Francoise Burel, Romain Carrié, Gaetan Lefebvre, Romain Georges, Bertrand Gauffre, David Giralt, Samuel Hilaire, Jesus Minano, Annie Ouin, Brigitte Poulin, Gavin Siriwardena, Yann Clough

Abstract

Biological pest control is in general positively affected by predatory arthropod diversity and thereby negatively by the loss of semi-natural habitats in farmlands. Increasing heterogeneity of cropland could offset negative effect on diversity, but the link between landscape heterogeneity, arthropods and pest suppression is not well known. Trait-based approaches could help a mechanistic understanding of this link. We tested for the first time whether landscape effects on biological pest control are mediated by arthropod traits using data from seven European regions. We found that biological control had a hump-shaped response to crop diversity within landscapes and increased with the dominance of omnivores in carabid communities. However, the crop diversity effect was not mediated by carabid traits. Further, mean body size of spider communities decreased with decreasing field size. Future landscape management should aim at increasing crop diversity with extensively managed crops to promote biological pest control.

Introduction

The worldwide loss of biodiversity threatens crop production by destabilising biological pest control (Newbold *et al.* 2015). This important ecosystem service, valued at $4.5 billion annually (Losey & Vaughan 2006) depends largely on predatory arthropods (Tscharntke *et al.* 2007). Declines in arthropods have been attributed to agricultural intensification, which operate at local and landscape scale. Increased pesticide use and loss of landscape heterogeneity have shown negative impacts on species diversity and biological control (Geiger *et al.* 2010). At a landscape scale, loss of landscape heterogeneity in Europe through removal of semi-natural habitats, reduction in number of crops grown and enlargement of fields to facilitate mechanisation are among the causes of biodiversity loss (Benton *et al.* 2003). Many studies support that semi-natural habitat in landscape enhances abundance and diversity of pest enemies and biological control (Chaplin-Kramer *et al.* 2011); most of them considering semi-natural habitats as a proxy for landscape heterogeneity. However, this view might simplify the reality in agricultural areas. Fahrig *et al.* (2011) pointed out that cultivated areas support many species, which use these habitats during their different stages of their lives. The authors introduced a new concept of crop heterogeneity, which include two components of compositional and configurational heterogeneity. The compositional heterogeneity can be defined as the diversity of crop types in a landscape, which provide diverse resources leading to landscape complementation (Dunning *et al.* 1992; Fahrig *et al.* 2011). The configurational heterogeneity is the degree of spatial arrangement of habitats, which can be measured as field size or the number of habitat edges. If increasing crop heterogeneity benefits biodiversity through landscape complementation, this holds a great opportunity to enhance biological pest control in landscape with little semi-natural habitats.

However, to date the few studies integrating this heterogeneity view have yielded mixed results. For example, Fahrig *et al.* (2015) found that smaller fields enhance diversity of several taxa including generalist predators such as spiders, but effects were not apparent for carabid beetles. Although Palmu *et al.* (2014) found that crop diversity enhanced carabid diversity. More recently, studies reported positive effects of temporal change in crop diversity on carabids (Bertrand *et al.* 2016b) and negative effect of increased average field size on carabid and spider diversity (Bertrand *et al.* 2016a). Nevertheless, no effects of field size was found on pest predation suggesting that effects on generalist predators did not down-scale on pest (Bertrand *et al.* 2016a).

It is now widely acknowledged that diversity of predators do not have unique predictable effects on pest suppression in agroecosystems (Straub *et al.* 2008). Their link to pest suppression may depend on species interaction within communities (Straub *et al.* 2008), but also on their different traits (e.g. Bell *et al.* 2008). A recent opinion paper highlighted that there is a crucial need of trait-based approaches to understand the biodiversity impacts on ecosystem services in agriculture (Wood *et al.* 2015). Research on trait based approaches on arthropods has started recently and are flourishing (Wood *et al.* 2015). Some recent studies focused on disentangling landscape composition and configuration on species traits, but did not focus on crop heterogeneity. For example, Gámez-Virués *et al.* (2015) found consistently across several taxa that loss of habitat diversity and configuration benefit arthropods with generalist traits like species with wide feeding range. Duflot *et al.* (2014) found that carabid species reproducing early in the season were favoured in open landscapes. Others investigated how traits may affect biological control, but these studies are rare. A recent study found that habitat preference and body size of spider, but not carabids determine their ability to reduce aphid pests in cereals (Rusch *et al.* 2015). Gagic *et al.* (2015) use a broader concept, trying to compare the contribution of single-traits (effect of dominant trait in communities) and multiple-traits (functional diversity or complementarity) for predicting multiple ecosystem services. The authors found out that trait approaches were better predictors of ecosystem services than species richness or abundance. This highlights that assembly of communities based on traits need to be considered when relating traits to ecosystem services.

Moreover, since landscape changes affect traits and to some extent traits affect ecosystem services, we expect that landscape change could have an impact on biological control through trait-mediated effect. Yet, none has tried to link landscape changes, changes in traits and their consequences on biological pest control at present. Although, some studies investigated the importance of trait-mediation in environmental change effects on ecosystem functioning (Laliberté & Tylianakis 2012; Lavorel *et al.* 2013; Barnes *et al.* 2014), none of them have used such an approach to relate changes in landscape composition and configuration to shifts in community trait composition and biological pest control.

Focusing on carabid beetle and spider communities and estimation of biological control in 342 landscapes across seven European regions, we investigated the landscape-wide crop compositional and configurational heterogeneity and semi-natural habitat cover effects on (1) dominant trait shifts at the community level, (2) arthropod functional diversity, (3) and their consequences on biological pest control in cereal fields. We expected that crop heterogeneity affect trait shifts within communities more strongly than functional diversity and that the effects had direct consequences on biological control.

Material and methods

Study area and sampling design

This study was carried out in seven regions within four European countries: Spain, France (four regions), Germany and U.K. (supplementary material Fig. S1). We selected in each region 1×1 km landscapes along orthogonal gradients of landscape crop composition and crop configuration heterogeneity using the method described in Pasher *et al.* (2013) and Fahrig *et al.* (2015). The crop composition was measured as the Shannon diversity index of crops cultivated in the sampled year (crop SHDI). The crop configuration was measured as the sum of field border length per area of crop cover in the landscape (FBD). Landscapes with high field border density were characterized by small fields and landscape with low field border density by large fields on average. In order to maximize gradient length of these heterogeneity measures, we selected landscapes dominated by agricultural land use (mean ± SEM: 84 ± 7%). We chose 342 landscapes across regions. We mapped as well all non-crop area in the landscape and classified all field margins (e.g. hedges, grassy strips), woodland and open grassy areas (e.g. unimproved grasslands, fallows) as semi-natural habitat (SNH). Within each landscape, three fields of major crops grown in the region were selected. For this study, we analysed only cereal fields (mainly wheat), which was the common crop grown in all regions. This resulted in 1 to 3 fields per landscape in 318 landscapes (Armorique: 36, Camargue: 33, Coteaux: 32, PVDS: 75, Lleida: 40, Göttingen: 52, East Anglia: 50).

Arthropod sampling

We sampled arthropods in all regions following a standardized protocol. In each region, sampling was carried out in two cropping seasons (2013 and 2014 or 2012 and 2013 for East-Anglia) on different fields and landscapes due to crop rotation. We sampled carabid beetles and spiders with pitfall traps. We established within each field two 50m long transects parallel to a semi-natural vegetated field margin, one at the field border and one 25m inside the field. At each end of the transects we placed a pitfall trap (9.5 mm diameter) protected by a roof. Each trap was filled with a water-salt solution (10g salt/L) and some odourless dish soap. The traps were opened twice for four days during the growing season. Carabid beetles and spider were stored in 70% ethanol. Then, carabids and adult spiders were identified to species level. We pooled arthropod counts at the field level within cropping seasons.

Estimation of biological control potential

We estimated biological control potential in cereal fields by measuring predation rates of aphids glued on labels (Geiger *et al.* 2010; Bertrand *et al.* 2016a). Three adult pea aphids *Acyrthosiphon pisum* were pasted with odourless spray glue on a 5×6 cm piece of dark sandpaper ("aphid label"). We placed 10 labels (30 aphids) in each cereal field at the same period pitfall traps were opened. Labels were positioned in two rows of five parallel to transects at 40 and 50m from field borders, to avoid interactions with pitfall traps (Fig. S1). The labels were fold like a tent to protect aphids from rain and pinned to the ground, with aphids facing downwards, so that ground-dwelling predators could access them. Predation rate were calculated based on the number of removed aphids after 24 hours exposition in the field. We pooled the data from both rounds per sampling year, except for East-Anglia (in 2012 and 2013) and Göttingen (in 2013), where data of the second round was missing.

Arthropod traits

We chose four groups of traits that were expected influencing predation function: body size, foraging strategy, dispersal capacity and reproduction (Bell *et al.* 2008; Woodcock *et al.* 2014; Rusch *et al.* 2015).

We collected information on average body length of males and females, diet preference, wing morphology and breeding season for carabid beetles (Table 1). Average body length of males and females, foraging mode, vertical stratum preference and ballooning capacity were used for spiders. The information for each trait was compiled mainly from databases. We used two trait databases: the Biological and Ecological functional Traits of Soil Invertebrates - BETSI database (Hedde *et al.* 2012) for both taxa and the carabids.org database (Homburg *et al.* 2014) for carabid beetles. Further literature and expert knowledge was used to complete gaps in the databases. This additional information was then stored in the BETSI database. We calculated a single-trait index, the community-weighted mean (CWM) for each trait. We excluded from the analysis rare species occurring less than five times in all regions and communities with less than five individuals caught per growing season. CWM is the mean trait value of the community, weighted by the abundance of species. Categorical traits were transformed into continuous or binary variable to be able to calculate CWM for each trait (Table 1). We also calculated a multiple-trait metric, the functional dispersion (FDis) within communities. This measures the variation or complementarity of traits within a community (Laliberté & Legendre 2010).

Data analysis

The objective of this study was to (1) disentangle the effects of crop composition (crop SHDI), crop configuration (FBD) and semi-natural habitat cover (SNH) on arthropod community structure of species with different traits, and to (2) test whether biological control potential was driven by landscape variables and (3) by carabid beetles community structure. We used piecewise structural equation models (SEM), which enable to model complex system with directed pathways, where variables can be response and predictor simultaneously. In contrast to traditional SEM, the piecewise approach allow to model complex systems using mixed effect models (Lefcheck 2016). First, we built a hypothetical path diagram representing cascading effects of variables (Fig. 1a). We constructed a path diagram for each taxon. The effects on biological control potential were only tested with carabid beetle communities, since spiders are not likely to prey on aphid labels according to expert knowledge (R. Gallé, pers. comm.). For spiders, we tested only the effects of landscape variables on community traits.

Second, we build individual mixed effect models with response variables being all endogenous variables in the path diagram (boxes with incoming arrows, Fig. 1a). Predictor variables (fixed effects) were all variables linked by a pathway to the response variables. We included nested random effects reflecting the spatial and temporal data structure: landscape nested in sampling year nested in region. We standardised (mean centred and scaled) all variables, except for predation rate modelled with binomial distribution error ('logit' link) using 'lme4' package 1.1-7 (Bates *et al.* 2015) for R (R Core Team 2015). Model overdispersion was corrected by adding a random intercept at the field level (Warton & Hui 2011). Functional dispersion and CWMs responses were modelled using 'nlme' package 3.1-125 (Pinheiro *et al.* 2016). Assumptions of residual normality and homogeneity of variance were visually checked in all models. CWMs and abundance variables were exponential or $\log_{10}$ transformed if needed to meet normal residual distribution. We corrected residual heterogeneity for using a fixed variance structure if necessary. We also added quadratic terms to test for non-linear effects and the two-way interaction between landscape variables on CWMs. We then performed a manual backward model selection to find the most relevant pathways to include in the SEMs. Based on the Akaike Information Criterion (AIC), we manually removed non-significant fixed effects respecting marginality until the difference in AIC did not exceed 2 (Burnham 2004). No variance inflation was detected in the models (all variance inflation factors < 3, Zuur *et al.* 2009).

Third, we included all relevant pathways in the SEM. We used the abundance of carabid beetles and spiders as a co-variable, since CWMs are weighted and thus dependent on abundance. We ensured for both SEMs that the ratio between the number of statistical units (fields) and the number of pathways was above 5 (d-rule; Grace *et al.* 2015). The spider dataset included 530 fields from all seven regions and the carabid dataset 436 fields from all regions except Lleida, which had too few communities of less than 5 individuals. We analysed the carabid data from fields where the biological control potential data was available, thereby reducing the number of included fields. To test the goodness-of-fit of the SEM systems, we used the Shipley's test of directed separation (dsep) measured by Fisher's C (Shipley 2009). The dsep tests whether variables which are not connected by pathways (independence claims) are statistically independent. The structured system is supported, if the dsep p-value > 0.05 (Lefcheck 2016). Since animal traits are naturally correlated between them, we set links between traits as correlated errors in the SEM. Correlated errors represent relationships between two variables, which are driven by the same underlying factor (Lefcheck 2016). SEMs were analysed with the piecewiseSEM package for R (Lefcheck 2016).

Results

We caught in total 19 375 carabid and 29 812 adult spider individuals across all regions. The arthropod communities represented 93 carabid and 195 spider species occurring more than five times across all regions.

Predation rates were in general high with an average of 71% of aphids removed (± 24% standard deviation). The SEMs fitted the data well, with a Fisher's C= 26.47 (p = 0.97) for carabid data and a Fisher's C = 10.5 (p = 0.84) for spider data (Fig. 1b-c). For a detailed result summary, see supplement S1.

The landscape-wide crop composition (crop SHDI), configuration (FBD) and the cover in semi-natural habitat (SNH) had direct effects on shifts in carabid and spider communities mean traits (Figs. 1b-c & 2c-h). Crop SHDI decreased the dominance of early breeders over late breeding carabid species, but this effect was more marked in small-field landscapes (i.e. high field border density) than in large-field landscapes (Figs. 1b, 2c & 3b). Decreasing field size had a non-linear negative effect on spider CWM body size (Figs. 1c, 2e & 3e). SNH cover decreased carabid CWM body size, while it increased body sizes of spider species. SNH affected positively spider CWM foraging mode by increasing the dominance of hunting spiders. Spiders ballooning ability was reduced with increasing SNH favouring rarely ballooning spiders over those able to balloon (Figs. 2h & 3h). The dominance of soil-dwelling species decreased indirectly with FBD, mediated by the abundance of spiders. In contrast, the functional dispersion (FDis) of carabid and spider community traits was not affected by landscape variables.

Results from the SEM with carabid data (Fig. 1b) revealed that the biological control potential in cereal fields was influenced by crop SHDI, carabid abundance and CWM diet. However, landscape variables effects on predation rates were not mediated by pathways linking to CWMs and FDis. Crop SHDI directly increased predation rates peaking at intermediated values of Crop SHDI (Fig. 2a). Predation rates slightly decreased when the omnivores' proportion decreased, until predatory carabids dominated the community (Fig. 1b, 2b, 3c). Carabid abundance had a positive effect on predation rates (Fig. 1b).

Table 1. Functional traits of carabid beetles and spiders and their attributed value for community weighted means (CWM) calculation.

Traits group	Trait	Value
Carabid beetle		
Body size	Body length in mm (average of males and females)	2 – 30.5
Foraging	Predator (dominantly carnivore)	1
	Omnivore	0.5
	Herbivore	0
Dispersal	Fully winged	1
	Wing dimorphic	0.5
	Short winged	0
Reproduction	Early breeder (spring)	1
	Late breeder (summer/ autumn or winter)	0
	Both early and late breeder	0.5
Spiders		
Body size	Body length in mm (average of males and females)	1.35 – 14
Stratum preference	Soil dwelling	0
	Soil and vegetation dwelling	0.5
	Vegetation dwelling	1
Foraging mode	Hunting	1
	Web builder	0
Dispersal	Ballooning *	1
	Uncommon ballooning **	0

* Species ballooning regularly as juvenile and/or adult

** Species reported as not ballooning in the literature. However, these reports often only take into account the inability of spiders to balloon as adults. Some of these species sometimes balloon as juveniles (Schirmel *et al.* 2012)

Figure 1. Tested hypothetical pathway diagram (a) of the landscape parameters effects on arthropod traits mediated biological control potential. SEM results for the landscape effects on carabid traits mediated biological control potential (b) and for the landscape effects on spider traits (c). For sake of clarity, only significant pathways are presented (P-value< 0.05). Conditional R^2 are presented for response variables. Pathway coefficients are standardized, except for those linked to predation rate ("logit" transformed). Path coefficients preceded by Q and L denote coefficients for quadratic and linear terms respectively. Double sided arrows show significant correlations between correlated errors variables.

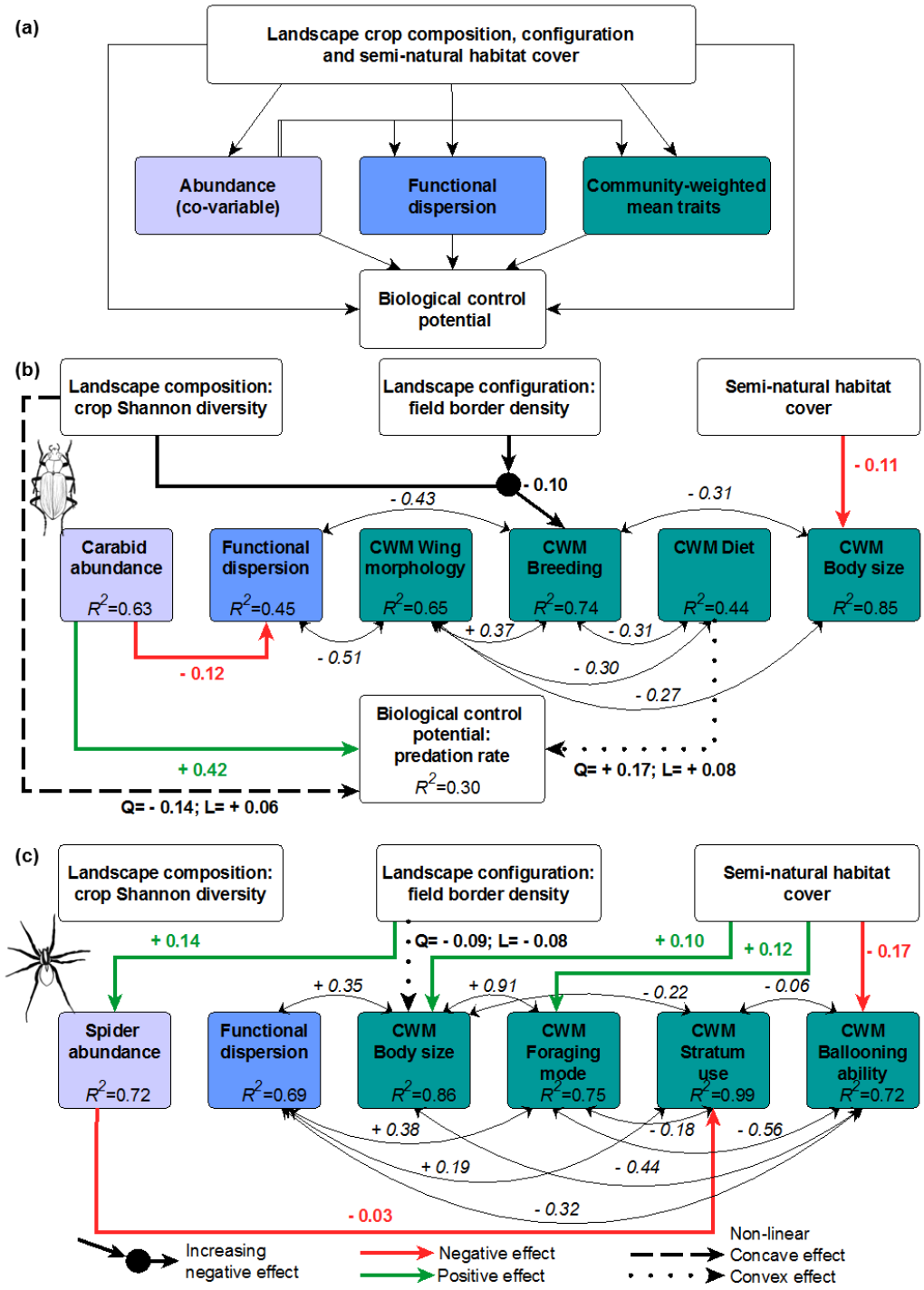


Figure 2. Model predictions for the significant pathways from the SEM with carabid data (a-d) and from the SEM with spider data (e-f). The main trends are predictions taking into account all random effects. The colored lines are predictions for regions with various intercepts. For illustrative purpose only, data points represent raw data for each region. Partial residuals are not shown.

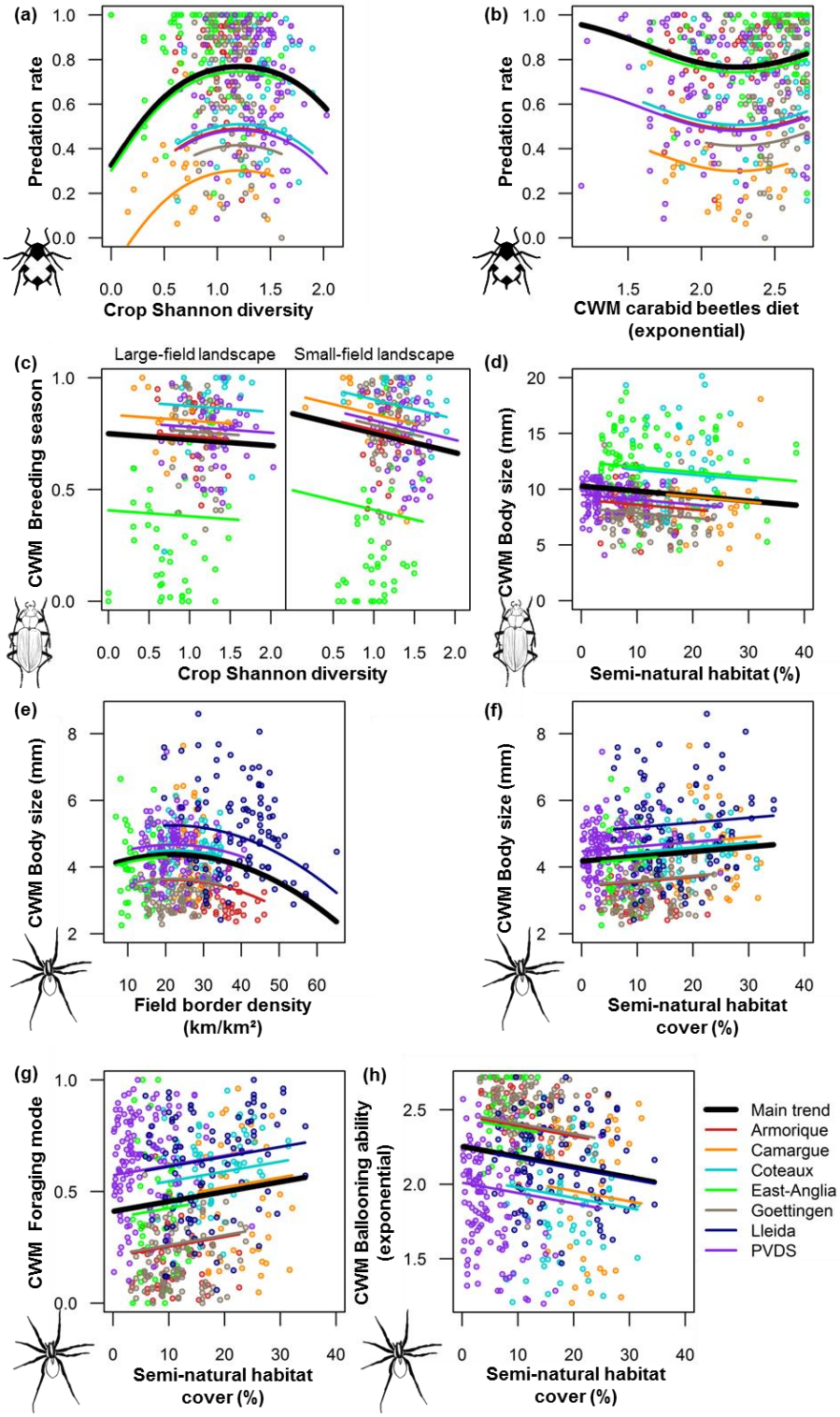
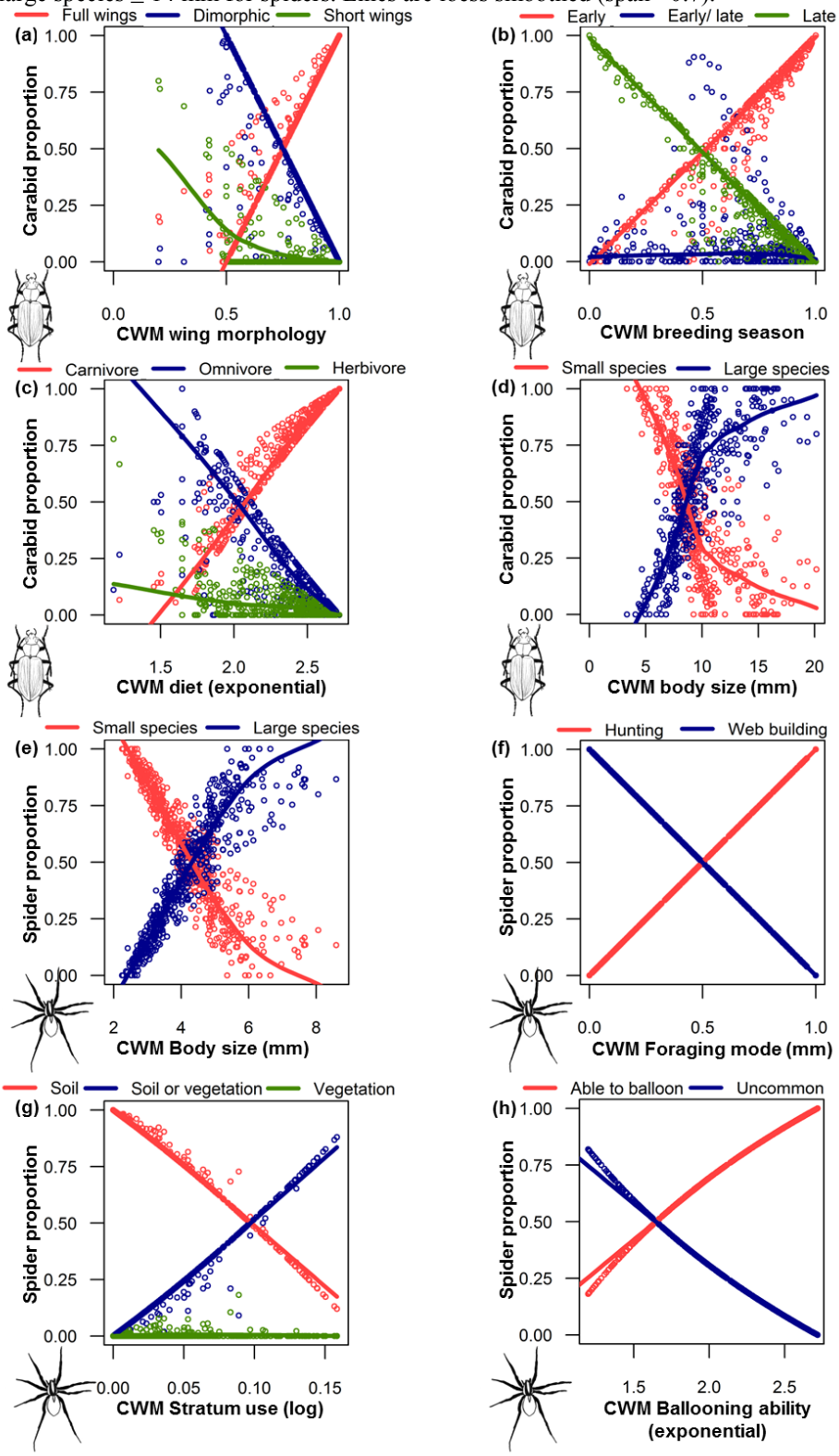


Figure 3. Relation between CWM and the proportional number of carabids (a-d) and spiders (e-h) within the communities for each trait level. For illustration purpose only, the trait body size was classified into small and large species: 2 ≤ small species < 8 mm; 8 < large species ≥ 30.5 mm for carabids and 1.35 ≤ small species < 3.7 mm; 3.7 ≤ large species ≥ 14 mm for spiders. Lines are loess smoothed (span= 0.7).



Discussion

We show for the first time a large-scale assessment of cascading effects of landscape crop heterogeneity on the ecosystem service of biological pest control across Europe, yielding several novel key insights. We demonstrate that landscape-wide crop heterogeneity, carabid abundance and trait identity influenced biological control potential. We found hump shaped effect of compositional crop heterogeneity, and positive effects of carabid abundance and dominance of omnivores on biological control potential in cereal fields. However, the landscape crop diversity effect was not mediated by abundance or trait identities and we found no effect of trait complementarity (functional dispersion). Hence, we show that trait effects on predation rates are rather supporting sampling effect than niche-complementarity effect theories, these effects running independently from landscape heterogeneity changes on communities. Besides, trait identities not directly linked to biological pest control were also affected by changes in landscape.

Compositional heterogeneity, carabid abundance and trait identity drives biological control

Our study shows that landscape-wide increase in crop diversity, independently of field border density had a hump shaped effect on biological control potential. Predation rates benefited from increased crop diversity only up to a certain point, in this case when the crop diversity index was around 1 (about 5 crop types per landscape). Natural enemies require many different resources throughout their lives, and are not bound to one particular crop such as the focal cereal crop. For example, many ground beetles and spiders are found in several crops in agricultural landscapes (Luff 1987; Samu & Szinetár 2002; Eyre *et al.* 2013). Many arthropods move over large distances and require several resources to complete their life-cycles (Schellhorn *et al.* 2015). However, crops are subject to periodic disturbances, which induced temporally unsuitability for natural enemies (Bianchi *et al.* 2006) leading to temporal resource discontinuity (Schellhorn *et al.* 2015). Increased crop diversity providing more resources may thus mitigate the temporal unavailability of certain crops boosting resource complementarity (Fahrig *et al.* 2011). This may in term benefit natural enemies and biological control. However, this beneficial effect became negative at higher crop diversity values. This may be due to an increase of crop resources which were more attractive for natural enemies than cereal crops. Though, such a dilution effect (Tscharntke *et al.* 2012) are unlikely in our regions since only the maize cover was strongly positively related to crop diversity in one region, Armorique ($r = 0.56$, Fig. SX). Maize receives comparatively more fertilizer and pesticide treatments (Kleijn & Verbeek 2000; Fagúndez *et al.* 2016) which is detrimental for natural enemies and biological control (Geiger *et al.* 2010). Higher levels of crop diversity may likely lead to increase in the cover of more intensively managed crop types which reverse the beneficial effect of compositional heterogeneity on biological control. Positive effects of crop diversity on soil-dwelling arthropods have be reported before (Billeter *et al.* 2008; Palmu *et al.* 2014; Bertrand *et al.* 2016b), but not non-linear effects. This may be due to a shorter range of crop diversity gradients in these studies which masked the hump shaped effect. It should be noted here, that compositional heterogeneity effect on biological control was not mediated through carabids and crop diversity had no effects on spiders. This suggest that other non-measured factors induced this effect such as predation by other soil-dwelling arthropods. Indeed, we observed that other generalist predators (e.g. Staphylinidae) consumed aphids on labels (personal observation). Another factor could have been the effect of species richness of ground-dwelling arthropods, which was not tested in this study. Species richness have shown positive effect on biological control, although such effects may depend on the strength of species interactions (Letourneau *et al.* 2009).

Carabid abundance had a strong positive effect on biological control, independently of species traits. Such purely abundance driven effects, independently from species traits were also found in dung removal process by dung beetles (Barnes *et al.* 2014). Further supporting our finding, Thies *et al.* (2011) reported that higher ground-predators to aphid prey ratios (i.e. higher predator abundance) decreased aphid populations as well. Although, in our study the abundance of carabid beetles and predation rates were positively related to the abundance of *Anchomenus dorsalis* and *Poecilus cupreus* ($P = 0.03$ for predation rate response to both species; result not shown), the two most abundant species present in all regions. These species are known to consume aphids in fields (Symondson 2002). Hence, abundance effect on biological control seems to support the sampling-effect hypothesis rather than a purely abundance driven effect. This hypothesis suggests that more species (in this case abundance) increase the probability of introducing more effective species which in turn positively affect ecosystem functioning or service (Letourneau *et al.* 2009; Wood *et al.* 2015).

Surprisingly, changes in diet from omnivore dominating to predator dominating communities had a slight overall negative effect on biological control potential. Although most carabid beetles are all to some degree polyphagous, some tend to be more predaceous, other prefer feeding on plant material and some consume both prey and plants (Holland 2002). We expected that the dominance of predator would positively affect biological control, since alternative plant resources can reduce prey consumption by omnivores (Frank *et al.* 2011).

But this effect may be context dependent (Eubanks & Denno 2000). Omnivory can lead to strong pest suppression as plant-based food can supplement feeding of omnivore and contribute to their persistence even when prey densities are low (Eubanks 2005). This trait identity effect also supports the sampling-effect hypothesis since it is the result of omnivory dominance (Wood *et al.* 2015). This is especially emphasized by the fact that the most numerous omnivore species was *Poecilus cupreus*.

As it is difficult to compare linear and non-linear effect sizes, we restrain from judging whether abundance, trait identities or landscape compositional heterogeneity had strongest effects on biological control potential. However, the slight changes in predation rates observed as response to CWM diet dominance suggest that carabid traits had the smallest effect on biological control. Likewise, functional dispersion, which had no effect on predation rates, may not support the complementarity hypothesis. This is partly in accordance with Gagic *et al.* (2015) who found that community weighted mean traits where more important than functional diversity for several ecosystem services. In addition, the authors found that trait identities and complementarity are more important than species abundance, which was not supported by our study. However, functional dispersion was negatively correlated to carabid abundance suggesting that low trait complementarity tended indirectly to favour biological control. This may again, be an artefact of increased abundance of certain species mentioned above which decreased FDis. This underlines the support of sampling effect hypothesis in this study.

Community assembly is affected by landscape metrics

Landscape metrics affected the dominant breeding season and body size of carabid beetles as well as spider abundance and the dominant body size, foraging mode and ballooning ability. These traits were not directly related to biological control potential, though changes in predation rates could be induced by landscape metrics through the strong correlations observed between traits.

The dominance of early breeding carabids (spring breeders) was favoured with increasing landscape-wide crop diversity in small-field landscapes. These species often hibernate as adults in semi-natural areas such as field margins or forests (Holland *et al.* 2009; Wamser *et al.* 2011). They colonise fields in spring from overwintering sites, whereas late breeding species (autumn) may not always rely on colonisation since they can hibernate in arable fields as larvae (Holland *et al.* 2009). Small-field landscape provide higher field interspersion which reduces the distances between patches (Fahrig *et al.* 2011) and could facilitate habitat spill-over and between patch movement for early breeders. Increasing crop diversity can moreover increase the resource complementarity in the landscape. Indeed, breeding and feeding traits were correlated. Dominance of early breeders coincided with the dominance of omnivores. Habitat complementation may thus be an advantage for early breeders which can find alternative food in other habitats. In addition, breeding season and body size were negatively correlated. Dominance of early breeders was related to smaller body sizes. Body size shift toward smaller species was related to increased semi-natural habitat cover. Thus, our results are in accordance with previous studies, which highlighted the importance of semi-natural habitats in the landscape for spring-breeders (Purtauf *et al.* 2005).

The landscape configurational heterogeneity had a positive effect on spider abundance, as previously reported by Bertrand *et al.* (2016a). The authors explained that landscape with smaller fields may facilitate spider colonisation in cereals. At the community level, we observed a shift towards smaller-sized species with decreasing field sizes in the landscape. Contrastingly, shifts towards larger-sized species were identified with higher availability of semi-natural habitats in the landscape. Smaller fields may facilitate spider movement between patches, whereas large-sized spiders, which correlated to lower ballooning ability, may rely more on semi-natural habitats than on changes in crop configurational heterogeneity. This may be in line with Birkhofer *et al.* (2015) who found that less disturbed areas favoured large-sized species with lower dispersal ability, underlining the sensitivity of large spider species to disturbance. This suggests that smaller field landscapes by facilitating spider dispersal cannot offset the negative effect that loss of semi-natural habitat could cause on large-sized spider species.

Conclusions

By assessing landscape crop heterogeneity on biological control potential across Europe, we provide three novel insights on mechanism driving arthropod-mediated ecosystem services. First, in contrast to previous studies demonstrating that biological pest control depends on semi-natural habitat cover (Geiger *et al.* 2010; Chaplin-Kramer *et al.* 2011), we showed that biological control depended on landscape-wide crop heterogeneity. Although, it should be noted here that our landscapes had high shares of cultivated area which may be representative for simplified landscapes, but not more complex ones. Second, the hump shaped effect of landscape-wide crop diversity on predation rates suggests that crop diversity may be beneficial up to a tipping point, until adding more of certain crops with intensive management practices reverse the effect.

We recommend therefore to promote crop diversity in landscapes by encouraging crop rotations where intensively managed crops are inter-cropped with less intensively managed crops such as leys (Palmu *et al.* 2014). Third, species sampling-effects rather than species complementarity drove biological control as well. High abundance of certain species, especially omnivores were related to high predation rates. This highlights that species have unequally efficient abilities to reduce pests and that this may depend on species interactions (Straub & Snyder 2006; Straub *et al.* 2008). Finally, crop diversity effects on biological control was not directly mediated through carabid beetle traits. However, higher crop diversity and smaller field sizes in landscapes favoured spring breeders which were also omnivores. In this sense, reducing field sizes in the landscape may indirectly enhance pest control.

Acknowledgements

This study was part of the FarmLand project funded by the ERA-Net BiodivERsA. Specific national funders were: French National Research Agency (ANR-11-EBID-0004), German Federal Ministry of Education and Research (BMBF) and Spanish Ministry of Economy and Competitiveness, part of the 2011 BiodivERsA call for research proposals. The funding scheme for UK was the UK Government Department of the Environment, Food and Rural Affairs (Defra, project WC1034). The author A.B.B. was supported by a scholarship from the German Academic Exchange Service (DAAD). We thank all farmers who allowed us to sample on their fields, and the many fieldwork-helpers. A special thank goes to Jonathan Lefchek for help with the statistics, Yvan Capowiez and Alain Pasquet for providing further expert knowledge and help with spider traits and Aline Marcastel which performed predation estimation in 2014 in Göttingen.

References

1.
Barnes, A.D., Emberson, R.M., Krell, F.-T. & Didham, R.K. (2014). The Role of Species Traits in Mediating Functional Recovery during Matrix Restoration. *PLoS ONE*, 9, e115385
2.
Bates, D., Mächler, M., Bolker, B. & Walker, S. (2015). Fitting Linear Mixed-Effects Models using lme4. *J. Stat. Softw.*, 67, 1–48
3.
Bell, J.R., Mead, A., Skirvin, D.J., Sunderland, K.D., Fenlon, J.S. & Symondson, W.O.C. (2008). Do functional traits improve prediction of predation rates for a disparate group of aphid predators? *Bull. Entomol. Res.*, 98, 587
4.
Benton, T.G., Vickery, J.A. & Wilson, J.D. (2003). Farmland biodiversity: is habitat heterogeneity the key? *Trends Ecol. Evol.*, 18, 182–188
5.
Bertrand, C., Baudry, J. & Burel, F. (2016a). Seasonal variation in the effect of landscape structure on ground-dwelling arthropods and biological control potential. *Basic Appl. Ecol.*
6.
Bertrand, C., Burel, F. & Baudry, J. (2016b). Spatial and temporal heterogeneity of the crop mosaic influences carabid beetles in agricultural landscapes. *Landsc. Ecol.*, 31, 451–466
7.
Bianchi, F.J.J.A., Booij, C.J.H. & Tscharntke, T. (2006). Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. *Proc. R. Soc. Lond. B Biol. Sci.*, 273, 1715–1727
8.
Billeter, R., Liira, J., Bailey, D., Bugter, R., Arens, P., Augenstein, I., *et al.* (2008). Indicators for biodiversity in agricultural landscapes: a pan-European study: Biodiversity in European Agro-ecosystems. *J. Appl. Ecol.*, 45, 141–150
9.
Birkhofer, K., Smith, H.G., Weisser, W.W., Wolters, V. & Gossner, M.M. (2015). Land-use effects on the functional distinctness of arthropod communities. *Ecography*, 38, 889–900
10.
Burnham, K.P. (2004). Multimodel Inference: Understanding AIC and BIC in Model Selection. *Sociol. Methods Res.*, 33, 261–304
11.

Chaplin-Kramer, R., O'Rourke, M.E., Blitzer, E.J. & Kremen, C. (2011). A meta-analysis of crop pest and natural enemy response to landscape complexity. *Ecol. Lett.*, 14, 922–932
12.
Duflot, R., Georges, R., Ernoult, A., Aviron, S. & Burel, F. (2014). Landscape heterogeneity as an ecological filter of species traits. *Acta Oecologica*, 56, 19–26
13.
Dunning, J.B., Danielson, B.J. & Pulliam, R.H. (1992). Ecological processes that affect populations in complex landscapes. *Oikos*, 65
14.
Eubanks, M.D. (2005). Predaceous herbivores and herbivores and herbivorous predators: the biology of omnivore-prey interactions. In: *Ecology of predator-prey interactions* (eds. Barbosa, P. & Castellanos, I.). Oxford University Press, New York
15.
Eubanks, M.D. & Denno, R.F. (2000). Host plants mediate omnivore-herbivore interactions and influence prey suppression. *Ecology*, 81, 936–947
16.
Eyre, M.D., Luff, M.L. & Leifert, C. (2013). Crop, field boundary, productivity and disturbance influences on ground beetles (Coleoptera, Carabidae) in the agroecosystem. *Agric. Ecosyst. Environ.*, 165, 60–67
17.
Fagúndez, J., Olea, P.P., Tejedo, P., Mateo-Tomás, P. & Gómez, D. (2016). Irrigation and Maize Cultivation Erode Plant Diversity Within Crops in Mediterranean Dry Cereal Agro-Ecosystems. *Environ. Manage.*, 58, 164–174
18.
Fahrig, L., Baudry, J., Brotons, L., Burel, F.G., Crist, T.O., Fuller, R.J., *et al.* (2011). Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecol. Lett.*, 14, 101–112
19.
Fahrig, L., Girard, J., Duro, D., Pasher, J., Smith, A., Javorek, S., *et al.* (2015). Farmlands with smaller crop fields have higher within-field biodiversity. *Agric. Ecosyst. Environ.*, 200, 219–234
20.
Frank, S.D., Shrewsbury, P.M. & Denno, R.F. (2011). Plant versus prey resources: Influence on omnivore behavior and herbivore suppression. *Biol. Control*, 57, 229–235
21.
Gagic, V., Bartomeus, I., Jonsson, T., Taylor, A., Winqvist, C., Fischer, C., *et al.* (2015). Functional identity and diversity of animals predict ecosystem functioning better than species-based indices. *Proc. R. Soc. B Biol. Sci.*, 282, 20142620–20142620
22.
Gámez-Virués, S., Perović, D.J., Gossner, M.M., Börschig, C., Blüthgen, N., de Jong, H., *et al.* (2015). Landscape simplification filters species traits and drives biotic homogenization. *Nat. Commun.*, 6, 8568
23.
Geiger, F., Bengtsson, J., Berendse, F., Weisser, W.W., Emmerson, M., Morales, M.B., *et al.* (2010). Persistent negative effects of pesticides on biodiversity and biological control potential on European farmland. *Basic Appl. Ecol.*, 11, 97–105
24.
Grace, J.B., Scheiner, S.M. & Schoolmaster, D.R. (2015). Structural equation modeling: building and evaluating causal models. In: *Ecological statistics: from principles to applications* (eds. Fox, G.A., Negrete-Yankelevich, S. & Sosa, V.J.). Oxford University Press, pp. 168 – 199
25.
Hedde, M., Pey, B., Auclerc, A., Capowiez, Y., Cluzeau, D., Cortet, J., *et al.* (2012). BETSI, a complete framework for studying soil invertebrate functional traits. Presented at the XVI ICSZ-International Colloquium on Soil Zoology, Coimbra
26.
Holland, J.M. (2002). *The agroecology of carabid beetles*. Intercept, Andover
27.
Holland, J.M., Birkett, T. & Southway, S. (2009). Contrasting the farm-scale spatio-temporal dynamics of boundary and field overwintering predatory beetles in arable crops. *BioControl*, 54, 19–33
28.
Homburg, K., Homburg, N., Schäfer, F., Schuldt, A. & Assmann, T. (2014). Carabids.org - a dynamic online database of ground beetle species traits (Coleoptera, Carabidae). *Insect Conserv. Divers.*, 7, 195–205

29.
Kleijn, D. & Verbeek, M. (2000). Factors affecting the species composition of arable field boundary vegetation. *J. Appl. Ecol.*, 37, 256–266
30.
Laliberté, E. & Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, 91, 299–305
31.
Laliberté, E. & Tylianakis, J.M. (2012). Cascading effects of long-term land-use changes on plant traits and ecosystem functioning. *Ecology*, 93, 145–155
32.
Lavorel, S., Storkey, J., Bardgett, R.D., de Bello, F., Berg, M.P., Le Roux, X., *et al.* (2013). A novel framework for linking functional diversity of plants with other trophic levels for the quantification of ecosystem services. *J. Veg. Sci.*, 24, 942–948
33.
Lefcheck, J.S. (2016). piecewiseSEM: Piecewise structural equation modelling in r for ecology, evolution, and systematics. *Methods Ecol. Evol.*, 7, 573–579
34.
Letourneau, D.K., Jedlicka, J.A., Bothwell, S.G. & Moreno, C.R. (2009). Effects of Natural Enemy Biodiversity on the Suppression of Arthropod Herbivores in Terrestrial Ecosystems. *Annu. Rev. Ecol. Evol. Syst.*, 40, 573–592
35.
Losey, J.E. & Vaughan, M. (2006). The economic value of ecological services provided by insects. *BioScience*, 56, 311–323
36.
Luff, M.L. (1987). Biology of polyphagous ground beetles in agriculture. *Agric Zool Rev*, 2, 237–278
37.
Newbold, T., Hudson, L.N., Hill, S.L.L., Contu, S., Lysenko, I., Senior, R.A., *et al.* (2015). Global effects of land use on local terrestrial biodiversity. *Nature*, 520, 45–50
38.
Palmu, E., Ekroos, J., Hanson, H.I., Smith, H.G. & Hedlund, K. (2014). Landscape-scale crop diversity interacts with local management to determine ground beetle diversity. *Basic Appl. Ecol.*, 15, 241–249
39.
Pasher, J., Mitchell, S.W., King, D.J., Fahrig, L., Smith, A.C. & Lindsay, K.E. (2013). Optimizing landscape selection for estimating relative effects of landscape variables on ecological responses. *Landsc. Ecol.*, 28, 371–383
40.
Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Core Team. (2016). *nlme: Linear and Nonlinear Mixed Effects Models*. Available at: http://cran.r-project.org/web/packages/nlme/. Last accessed 18 November 2016
41.
Purtauf, T., Roschewitz, I., Dauber, J., Thies, C., Tscharntke, T. & Wolters, V. (2005). Landscape context of organic and conventional farms: Influences on carabid beetle diversity. *Agric. Ecosyst. Environ.*, 108, 165–174
42.
R Core Team. (2015). *R: A language and environment for statistical computing*. Available at: https://www.R-project.org/. Last accessed 18 November 2016
43.
Rusch, A., Birkhofer, K., Bommarco, R., Smith, H.G. & Ekbom, B. (2015). Predator body sizes and habitat preferences predict predation rates in an agroecosystem. *Basic Appl. Ecol.*, 16, 250–259
44.
Samu, F. & Szinetár, C. (2002). On the nature of agrobiont spiders. *J. Arachnol.*, 30, 389–402
45.
Schellhorn, N.A., Gagic, V. & Bommarco, R. (2015). Time will tell: resource continuity bolsters ecosystem services. *Trends Ecol. Evol.*, 30, 524–530
46.
Schirmel, J., Blindow, I. & Buchholz, S. (2012). Life-history trait and functional diversity patterns of ground beetles and spiders along a coastal heathland successional gradient. *Basic Appl. Ecol.*, 13, 606–614
47.
Shipley, B. (2009). Confirmatory path analysis in a generalized multilevel context. *Ecology*, 90, 363–368
48.
Straub, C.S., Finke, D.L. & Snyder, W.E. (2008). Are the conservation of natural enemy biodiversity and biological

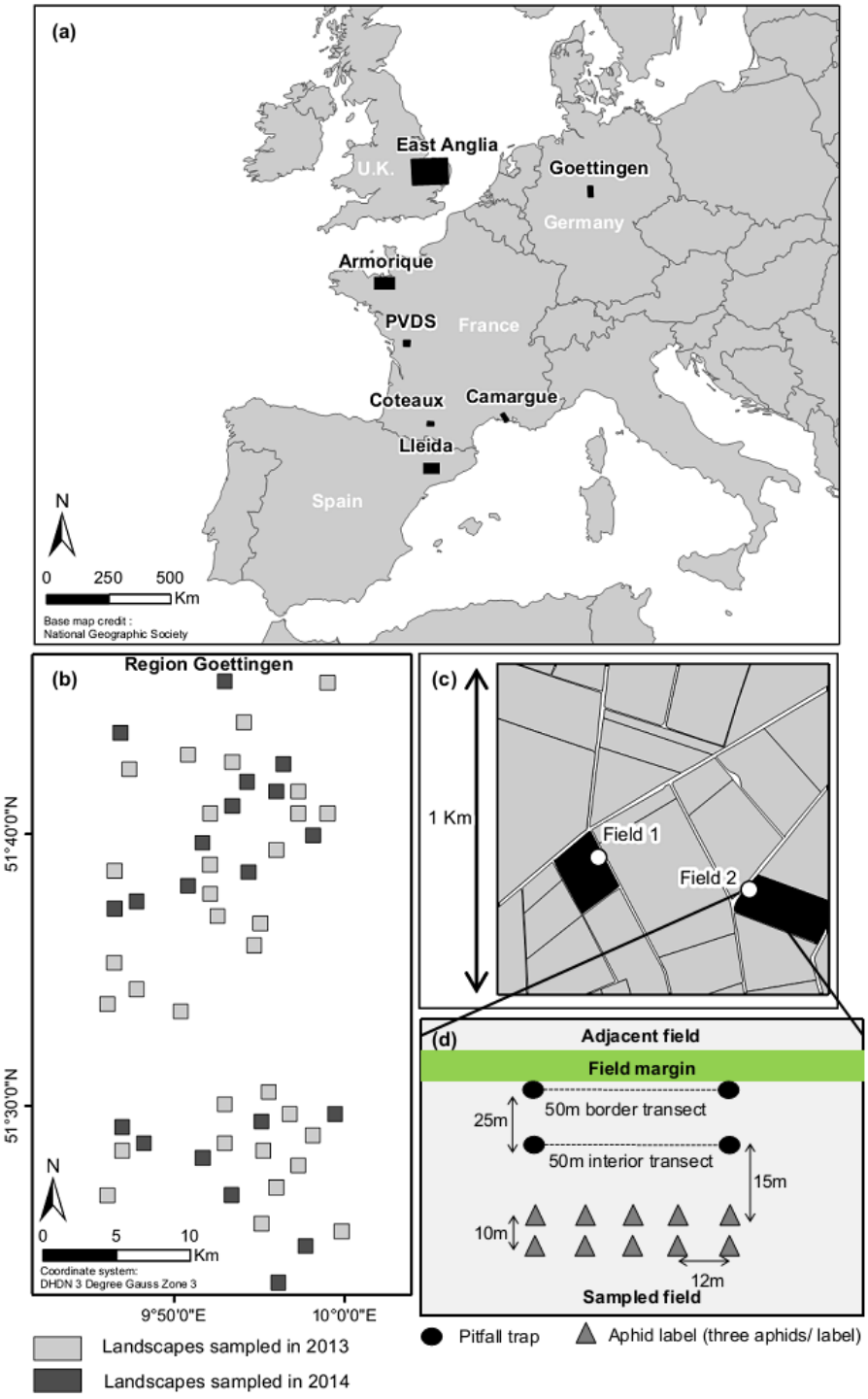
control compatible goals? *Biol. Control*, 45, 225–237
49.
Straub, C.S. & Snyder, W.E. (2006). Species identity dominates the relationship between predator biodiversity and herbivore suppression. *Ecology*, 87, 277–82
50.
Symondson, W.O.C. (2002). Diagnostic techniques for determining carabid diets. In: *The agroecology of carabid beetles* (ed. Holland, J.M.). Intercept, Andover
51.
Thies, C., Haenke, S., Scherber, C., Bengtsson, J., Bommarco, R., Clement, L.W., *et al.* (2011). The relationship between agricultural intensification and biological control: experimental tests across Europe. *Ecol. Appl.*, 21, 2187–2196
52.
Tscharntke, T., Bommarco, R., Clough, Y., Crist, T.O., Kleijn, D., Rand, T.A., *et al.* (2007). Conservation biological control and enemy diversity on a landscape scale. *Biol. Control*, 43, 294–309
53.
Tscharntke, T., Tylianakis, J.M., Rand, T.A., Didham, R.K., Fahrig, L., Batáry, P., *et al.* (2012). Landscape moderation of biodiversity patterns and processes - eight hypotheses. *Biol. Rev.*, 87, 661–685
54.
Wamser, S., Dauber, J., Birkhofer, K. & Wolters, V. (2011). Delayed colonisation of arable fields by spring breeding ground beetles (Coleoptera: Carabidae) in landscapes with a high availability of hibernation sites. *Agric. Ecosyst. Environ.*, 144, 235–240
55.
Warton, D.I. & Hui, F.K.C. (2011). The arcsine is asinine: the analysis of proportions in ecology. *Ecology*, 92, 3–10
56.
Wood, S.A., Karp, D.S., DeClerck, F., Kremen, C., Naeem, S. & Palm, C.A. (2015). Functional traits in agriculture: agrobiodiversity and ecosystem services. *Trends Ecol. Evol.*, 30, 531–539
57.
Woodcock, B.A., Harrower, C., Redhead, J., Edwards, M., Vanbergen, A.J., Heard, M.S., *et al.* (2014). National patterns of functional diversity and redundancy in predatory ground beetles and bees associated with key UK arable crops. *J. Appl. Ecol.*, 51, 142–151
58.
Zuur, A.F., Ieno, E.N., Walker, N., Saveliev, A.A. & Smith, G.M. (2009). *Mixed effects models and extensions in ecology with R*. Statistics for Biology and Health. Springer New York, New York, NY

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Fig. S1. Sampling site location and within-field sampling design.
Fig. S2. Carabid and spider abundance effect on SEM response variables.
Supplement S1. SEM pathway result summary

Fig. S1. Location of the seven studied regions (a) and example of selected landscapes in 2013 and 2014 in the region of Goettingen (b). The detail of a 1×1 km landscape (c) and the sampling design within one of the two selected cereal fields/ landscape (d).



Supplement S1. Pathway coefficients and 95% confidence interval for the SEM with carabid and biological control potential data (a) and the SEM with spider data (b). Significant pathways are in bold characters.

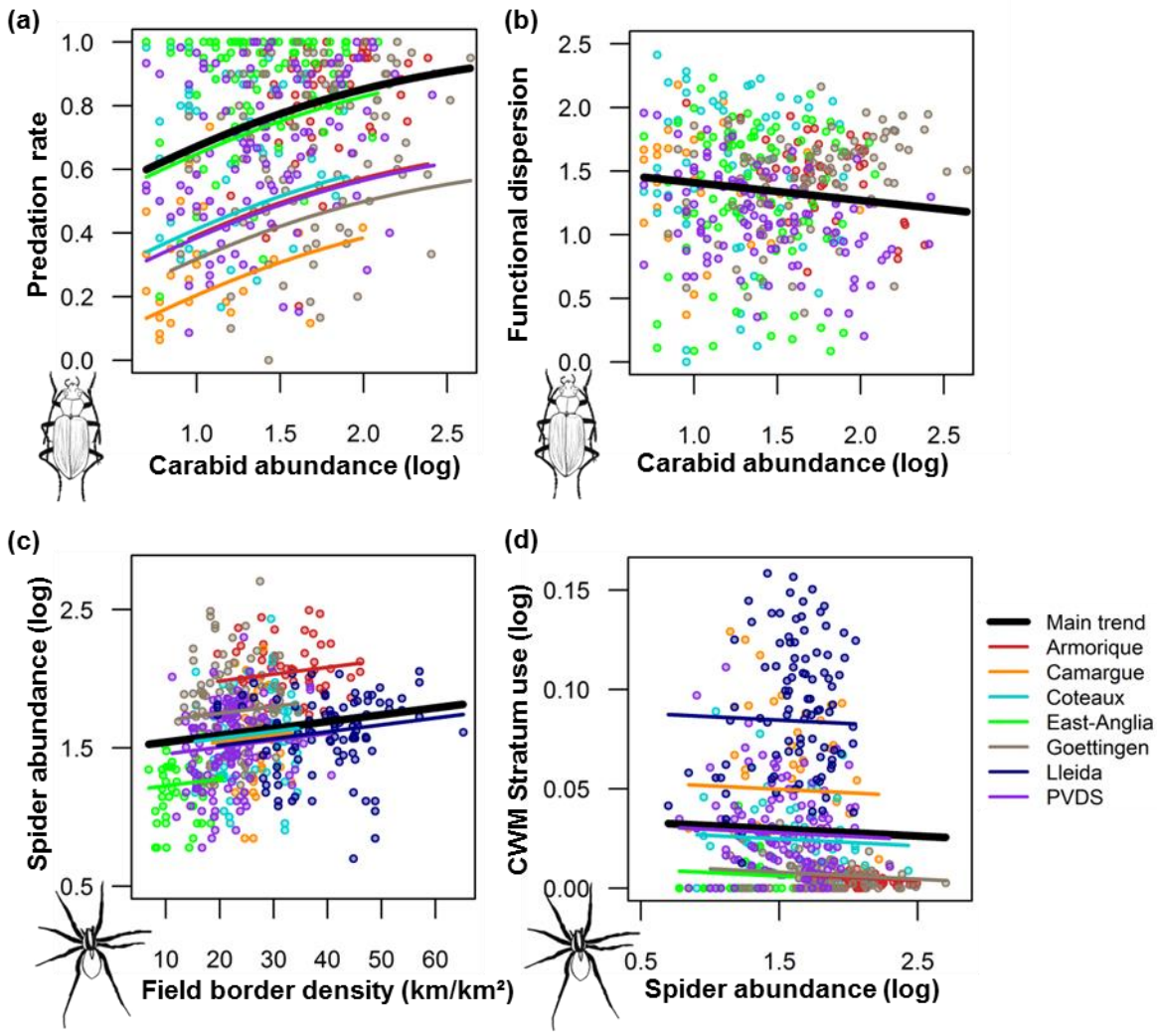
(a)

Response	Predictor	Path coeff. ± 95% confidence interval	P value
Predation rate	Carabid abundance	0.42 ± 0.16	**< 0.001**
	CWM Diet (Q)	0.17 ± 0.12	**0.006**
	Crop SHDI (Q)	-0.14 ± 0.11	**0.012**
	FBD × CWM Body size	-0.16 ± 0.19	0.102
	FBD × CWM Wing morphology	-0.15 ± 0.18	0.103
	Fdis (Q)	-0.09 ± 0.11	0.122
	Crop SHDI × FDis	0.11 ± 0.14	0.147
	Crop SHDI × FBD	0.12 ± 0.17	0.168
	CWM Body size	0.11 ± 0.2	0.273
	CWM Wing morphology	-0.13 ± 0.26	0.340
	CWM Diet	0.08 ± 0.22	0.496
	Crop SHDI	0.06 ± 0.18	0.521
	FBD	0.07 ± 0.23	0.537
	Fdis	-0.02 ± 0.21	0.883
	CWM Breeding	-0.01 ± 0.25	0.971
Carabid abundance	SNH	0.02 ± 0.13	0.834
CWM Body size	SNH	-0.12 ± 0.11	**0.029**
CWM Diet	Carabid abundance	0.07 ± 0.1	0.142
CWM Breeding	Crop SHDI × FBD	-0.1 ± 0.09	**0.016**
	FBD	0.11 ± 0.12	**0.070**
	SNH	0.08 ± 0.11	0.153
	Carabid abundance	0.05 ± 0.08	0.236
	Crop SHDI	-0.04 ± 0.09	0.458
CWM Wing morphology	Crop SHDI	-0.07 ± 0.09	0.133
Fdis	Carabid abundance	-0.13 ± 0.11	**0.020**
	SNH	0.11 ± 0.13	0.100
	Crop SHDI	0.09 ± 0.12	0.117

(b)

Response	Predictor	Path coeff. ± 95% confidence interval	P value
Spider abundance	StTBL	0.14 ± 0.14	**0.041**
CWM Body size	I(StTBL^2)	-0.1 ± 0.07	**0.005**
	StSN	0.1 ± 0.1	**0.040**
	StTBL	-0.08 ± 0.11	0.144
CWM Foraging mode	StSN	0.13 ± 0.11	**0.020**
	I(StTBL^2)	-0.05 ± 0.06	0.130
	StTBL	-0.06 ± 0.13	0.346
CWM Stratum use	StLogAbund	-0.04 ± 0.03	**0.015**
	StSN	0.03 ± 0.03	0.055
CWM Ballooning ability	StSN	-0.17 ± 0.11	**0.002**
	I(StSN^2)	0.07 ± 0.07	0.065
StFDis	StLogAbund	-0.07 ± 0.08	0.076

Fig. S2. Graphical display of significant pathways linked to the co-variables carabid abundance (a, b) and spider abundance (c, d). Lines are predictions based on mixed effects models. The main trend lines are global predictions taking into account all random effects. Coloured lines are predictions for the different regions. Regional lines are superposed when the main trend is displayed only (b).



CHAPTER 4
Cereal aphids, their enemies and biological control are driven by complex interactions between landscape-wide cropland composition, configuration and inter-annual heterogeneity

Submitted to Journal of Applied Ecology

Aliette Bosem Baillod, Teja Tscharntke, Yann Clough and Péter Batáry

Authors' contributions
A.B.B., T.T., Y.C. and P.B. developed the conceptual foundation of the manuscript. A.B.B. collected and analysed data. A.B.B wrote the manuscript and T.T., Y.C. and P.B. contributed to revisions.

Summary

1. Agricultural landscapes are characterised by dynamic crop mosaics changing in composition and configuration over space and time. While semi-natural habitat has been often shown to contribute to pest reduction by biological control, the effects of increasing landscape heterogeneity with cropland has been disregarded. Here, we examine how cereal aphids, their enemies and biological control are affected by the composition and configuration of the crop mosaic and its inter-annual change due to crop rotation.
2. We studied the abundance of cereal aphids, natural enemies and aphid parasitism over two years on 51 winter wheat fields. Arthropods were monitored at three distances (0, 10, 30m) from field border. Fields were embedded in landscapes of 1 km diameter selected along orthogonal gradients of compositional crop heterogeneity (crop diversity), configurational heterogeneity (field border and grassy field boundary length) and inter-annual change in cover of aphid host habitats (cereal, maize and grassland). We aimed to disentangle spatial and temporal heterogeneity effects through these independent landscape gradients.
3. Aphid densities were lower in landscapes with smaller field size (more field border length) coupled with high amount of grassy field boundaries. Aphid densities decreased also in landscapes with higher crop diversity when the cover of aphid host habitat had decreased from the year before. Aphid natural enemy densities increased with the length of grassy field boundary. Biological control through parasitism decreased with the inter-annual expansion in aphid host habitat, but only in landscape with small field size.
4. *Synthesis and applications*. Our study shows for the first time that cereal aphids can be reduced by optimizing the composition, configuration and temporal heterogeneity of the crop mosaic. We highlight the value of maintaining small field size in agricultural landscapes and high densities of grassy boundaries for reducing aphid abundance. Landscape-wide crop diversification can reduce aphids as well.

Keywords: aphid parasitism, crop rotation, edge effect, field size, field margin, predator-prey ratio, spatial heterogeneity, temporal heterogeneity, landscape configuration, landscape composition

Introduction

Pest control is a major issue in agricultural production and the use of pesticides to control pests is not environmentally sound. Insecticides applications have negative effects on pest's natural enemies (Geiger *et al.* 2010) and can lead to pest outbreaks through reduced biological control (Pimentel 2005). Natural enemies are important for regulating pest populations and promoting them may be an effective alternative to reduce pesticides applications (Pimentel 2005; Jonsson *et al.* 2008). Alongside pesticides' use, the land use changes of the last decades in agricultural landscapes had adverse effects on biodiversity of natural pest enemies and ecosystem services such as pest biological control (Rusch *et al.* 2010; Geiger *et al.* 2010; Bommarco, Kleijn & Potts 2013). Examples of land use change in Europe are the enlargement of fields, the decrease of crop diversity (i.e. fewer crops grown) and the loss of semi-natural habitats and landscape elements (e.g. hedges, grassy margins).

In spatially and temporally dynamic agricultural landscapes, semi-natural landscape elements have been shown to benefit natural enemies and biological control (Chaplin-Kramer *et al.* 2011). Indeed, while the crop mosaic undergoes regular compositional changes mainly due to crop rotation, which alter spatial and temporal heterogeneity (Vasseur *et al.* 2013; Schellhorn, Gagic & Bommarco 2015), semi-natural landscape features are rather stable in time. However, it has been recently suggested that this spatial and temporal crop heterogeneity may affect biodiversity and associated ecosystem services (Fahrig *et al.* 2011; Vasseur *et al.* 2013). The spatial heterogeneity of the crops can be described both by its composition in terms of different crops (e.g. crop diversity) and its spatial arrangement (e.g. average field size). The temporal crop heterogeneity describes changes in crop patterns due to annual succession of crops. In present studies the effects of landscape compositional and configurational crop heterogeneity are rarely disentangled (Fahrig *et al.* 2011) probably because they are typically highly correlated in agricultural landscapes (Pasher *et al.* 2013). A few studies have nonetheless disentangled both heterogeneity components and found positive effects of crop diversity (Palmu *et al.* 2014; Bertrand, Burel & Baudry 2016) and configuration (edge density or mean field size) on generalist predatory arthropods and biological control (Östman, Ekbom & Bengtsson 2001; Palmu *et al.* 2014; Fahrig *et al.* 2015; Bertrand, Burel & Baudry 2016). The long-term increase in crop diversity over multiple years was shown to positively affect natural enemies as well (Bertrand, Burel & Baudry 2016). Thus, increasing landscape crop compositional, configurational and temporal heterogeneities are expected to have positive effects on natural enemies and biological control and negative effects on pests.

Despite generally positive effects of landscape-wide semi-natural habitats and crop heterogeneity on arthropods, it does not translate into consistent negative effects on pest abundance (Chaplin-Kramer *et al.* 2011).

A possible reason is the fact that most studies do not take into account landscape-wide crop patterns that shape resource availability for pests (Veres *et al.* 2013). Landscape composition can affect pest through changes in the amount of host plant area. Two main hypotheses may explain this effect. The resource concentration hypothesis (Root 1973) predicts that pest densities increase with increasing area of host plants. Reasons for this effect are a higher pest immigration rate in concentrated host areas (monoculture) and a longer tenure time of pests explained by "appropriate" and "inappropriate landing" of herbivore on host or non-host plants (Finch & Collier 2000). Another contradicting idea is the landscape-moderated crowding and dilution hypothesis (Tscharntke *et al.* 2012). Crowding occurs when host crop area decreases and pests increase on remaining host area. A reverse effect, pest dilution, can be found when local pest abundance decreases with increasing host area (Grez *et al.* 2004). A review by Veres *et al.* (2013) reports contradictory results of host area change on pests in landscapes. The few studies reporting such effects support either dilution or crowding rather than resource concentration effects. Additionally, the rarely considered temporal heterogeneity of landscapes can also affect pests and biological control. For example, Zhao *et al.* (2013a) found that an inter-annual increase in wheat cover resulted in decreased cereal aphid densities in the study year, supporting the dilution hypothesis. Further, configurational heterogeneity of crops such as the size of fields grown with pests' host-plant may affect pest densities as well. Segoli & Rosenheim (2012) predicted that densities of pests with high reproductive rates and rapid field colonisation ability should increase with field size if the natural enemies concentrate close to field borders. Thus, measuring arthropods' within-field distributions (pest and enemies) is important to understand potential landscape effects. If field size effects are related to host crop area, interactions between compositional and configurational heterogeneity of crops are expected.

Our study system focuses on cereal aphids, their vegetation-dwelling predators and biological control through parasitism. In central Germany (similarly to other European regions), intensive agricultural landscapes are dominated by cereals and increasing maize cultivation area (Steinmann & Dobers 2013). Cereal aphids feed on several plants such as cereals , maize and grasses in general (*Poaceae* family), which occur in high amount in grasslands and grassy field boundaries (Hand 1989). Cereal aphids can switch between host crops within the growing season (Vialatte *et al.* 2006). Therefore it is important to take into account temporal landscape changes across all suitable habitats for aphids, rather than focusing only on the main crop host (e.g. Zhao *et al.* 2013a).

This study is the first one aiming to disentangle effects of landscape crop composition, configuration and temporal changes alongside within-field scale effect on cereal aphids, their vegetation- dwelling predators and biological control through aphid parasitism in crop mosaics. We hypothesized that (1) within-field densities of vegetation- dwelling predators and parasitism rates should be higher at field borders since adjacent grassy boundaries provide overwintering places, shelter and alternative resources for arthropods (edge effect hypothesis, Bianchi, Booij & Tscharntke 2006), while cereal aphid densities should be higher in field interiors (Segoli & Rosenheim 2012); (2) landscape composition measured by crop diversity should have a positive effect on natural enemies of aphids by providing different resources leading to landscape complementation (Fahrig *et al.* 2011), and a positive effect on aphids as landscapes with a more diverse crop composition may reduce host crop availability and lead to a crowding effect; (3) landscape inter-annual change in habitat cover suitable for aphids may reduce arthropod densities when the cover increases from the previous season when compared to the actual season (i.e. dilution and crowding effects); (4) landscape configuration measured by mean field size should have a negative effect on aphid densities when field size is reduced; and (5) the landscape configuration co-variable measured by the length of grassy field boundaries should have an overall positive effect on arthropods (in accordance to the edge effect hypothesis).

Material and method

Study site and design

In 2013 and 2014, aphid and predatory arthropods were monitored in winter wheat fields, in a 600 km² area within the districts of Göttingen (51°32'N, 9°54'E) and Northeim (51°42'N, 9°59'E), Lower Saxony, Germany. A total of 51 winter wheat fields (n = 31 in 2013; n = 20 in 2014) were selected along independent gradients of landscape wide crop diversity and field border density within a sector of 1 km diameter around wheat fields (see Fig. S1 in Supporting Information). Selected fields were different between years due to crop rotation. The wheat fields were conventionally managed with an average of 193 kg nitrogen.ha^{-1} and with five pesticide treatments. The last treatment was applied 3 to 4 weeks before arthropod sampling. Selected landscapes were dominated by cereals (58%, mainly winter wheat and barley), followed by non-grassy annual crops (24%, mainly oilseed rape and sugar beet), maize (9%), grassland (8%, mainly permanent meadows) and other perennial crops (1%, clover ley and orchards). Grassy boundaries were the major habitat interspersed between cropped fields. Selected landscapes had a high share of crop cover (85% on average, see Table S1) in order to minimise potential effects of semi-natural habitats on arthropods. The compositional heterogeneity of crops was measured using the Shannon diversity (hereafter SHDI) index of crops cultivated in the sampling year.

For calculating the index, crops were classified into the five above mentioned classes (cereal, maize, grassland, non-grassy annual crops and other perennial crops). The configuration heterogeneity of crops was measured as the sum of field perimeter within one landscape sector. Landscapes with high field border length (hereafter FBL) were characterised by small fields and landscape with low field border by large fields on average. Indeed, field border length was negatively correlated to the average field size in the landscape (Spearman rho= - 0·89). An additional configurational landscape metrics measured was the grassy boundary length (hereafter GBL). This metric measured the density of boundaries characterized by grassy verges along agricultural driveways between fields. The temporal heterogeneity was measured as the inter-annual change in aphid habitat cover (hereafter % ΔHab). Aphid habitat cover included all grassy crops (cereal, maize) and grasslands providing host plants for cereal aphids (Hand 1989; Leather 1993). The inter-annual cover change was calculated as follows:

$\%\ \Delta Hab = \%\ Habitat_{year\ t} - \%\ Habitat_{year\ t-1}$,

where $\%\ Habitat_{year\ t}$ and $\%\ Habitat_{year\ t-1}$ were the percentage cover in the studied year and the preceding year respectively (Thies, Steffan-Dewenter & Tscharntke 2008). A detailed statistical summary of the landscape metrics can be found in Table S1. Land use was mapped from a field survey for the sampling years and from field-level data provided by the Agricultural Ministry of Lower Saxony (Servicezentrum Landentwicklung und Agrarförderung Niedersachsen) for the preceding years.

Aphid, natural enemies and parasitism sampling

Aphids, parasitized aphids (mummies) and vegetation dwelling predators were surveyed in conventional wheat fields twice, during the flowering and milk ripening stages of winter wheat in June and July. Three 50 m transects were established parallel to the grassy boundary at the field border (first wheat row), at 10 m and 30 m into the field (Fig.1). Along each transect, three spots of 10 wheat shoots were selected randomly (30 shoots per transect in total). Aphids and predatory arthropods were counted by screening the shoot from ground to the top of the spike. Aphids were identified to species and predatory arthropod to family level. Arthropod densities were calculated per transect and pooled over flowering and milk ripening stages (sum of densities per 60 shoots per transect) to avoid too many zeros in the dataset. Predatory arthropods occurred in low numbers and were therefore pooled over families. Predator-prey ratio ($D_{predators}/D_{aphids}$) as well as parasitism rate ($D_{mummies}/D_{aphids}$) were calculated, where $D_{predators}$, D_{aphids} and $D_{mummies}$ represent predator, aphid and mummies densities respectively.

Statistical analysis

We analysed the effect of within-field position (border, 10m and 30m transects) and the two-way interactive effects between the four landscape metrics (crop Shannon diversity, % ΔHab, field border and grassy field boundary length) on the response variables aphid density, predator density, predator-prey ratio and parasitism rates. We used linear and generalised linear mixed-effects models with the following random structure for each model: fields nested in years. Aphid density and predator-prey ratio were square root transformed for achieving normal distribution of model residuals and modelled using 'nlme' package 3.1-120 (Pinheiro *et al.* 2016) for R (R Core Team 2015). Residual heterogeneity was corrected by adding an exponential variance structure of covariate. Predator densities and parasitism rates were modelled using 'lme4' package 1·1-7 (Bates *et al.* 2015) with poisson and binomial errors distribution respectively. Predator-prey ratio and parasitism rates had some extreme outliers (one predator-prey ratio observation = 1; four parasitism rate observations > 17%), which we removed before model fitting. We standardised (mean centred and scaled) landscape metrics for each model. Models presented neither overdispersion nor multicollinearity in the independent variables (variance inflation factor below 3, Zuur *et al.* 2009). Landscape metrics were not or weakly correlated (Spearman $|rho| \leq 0{\cdot}4$; Table S2). We applied a multimodel inference approach to obtain robust parameter estimates using "MuMIn" package 1.15.6 (Barton 2016). Model averaging was done on the model set with $\Delta AICc < 2$ (Burnham & Anderson 2004)

Results

A total of 13656 aphids were counted in the 51 wheat fields. Aphids were dominated by the species *Sitobion avenae* Fabricius (76·9 %) followed by *Metopolophium dirhodum* Walker (20·2 %), *Rhopalosiphum padi* Linnaeus (0·1 %) and parasitized aphids (2·9 %). Parasitism rates and predator density were generally low. A total of 211 aphid predators were counted, mainly *Syrphidae* (54·5 %, mostly larvae), followed by *Araneae* (34·1 %, *Linyphiidae*), *Chrysopidae* (10·0 %, mostly larvae) and *Coccinellidae* (1·4 %, mostly larvae). See Table S4 for a detailed summary of arthropod densities.

Local scale: within field position

Aphid density was lower at the field borders than inside the fields, although no significant density difference was detected between 10 and 30 m within the field (Figs 1& 2a). Parasitism rate followed the same trend as aphid densities (Figs 1& 2b). Predator density was not significantly related to within-field position, while predator-prey ratios were significantly lower at 10 m from the field border, although the difference in ratio was minor (0·01 predators per aphid, Fig. 2c). Within-field position variable showed in general stronger effects on response variables compared to landscape variables (Fig.1). A more detailed summary of model results with statistics can be found in the Table S3.

Spatial and temporal effects

Aphid densities were four times higher with increasing crop diversity when the aphid habitat cover was higher in the sampled year compared to the previous year (positive % ΔHab, Figs 1& 3a). In contrast, aphid densities were divided by four with increasing crop diversity when % ΔHab decreased. Aphid densities decreased with increasing FBL when the amount of GBL was high (Figs 1& 3d). In contrast, aphids almost doubled in landscapes with increasing FBL (i.e. smaller fields) and low amount of GBL (Fig. 3d).

Predator densities decreased with increasing FBL when the amount of GBL was high (Figs 1& 4a), while predator densities did not vary with increasing FBL (i.e. smaller fields) and low amount of GBL (Fig. 4a). In contrast, predator-prey ratios were not affected by landscape variables. Parasitism rates slightly increased by 1% with increasing % ΔHab when FBL was low. The reverse trend occurred when FBL was high (Fig. 4b).

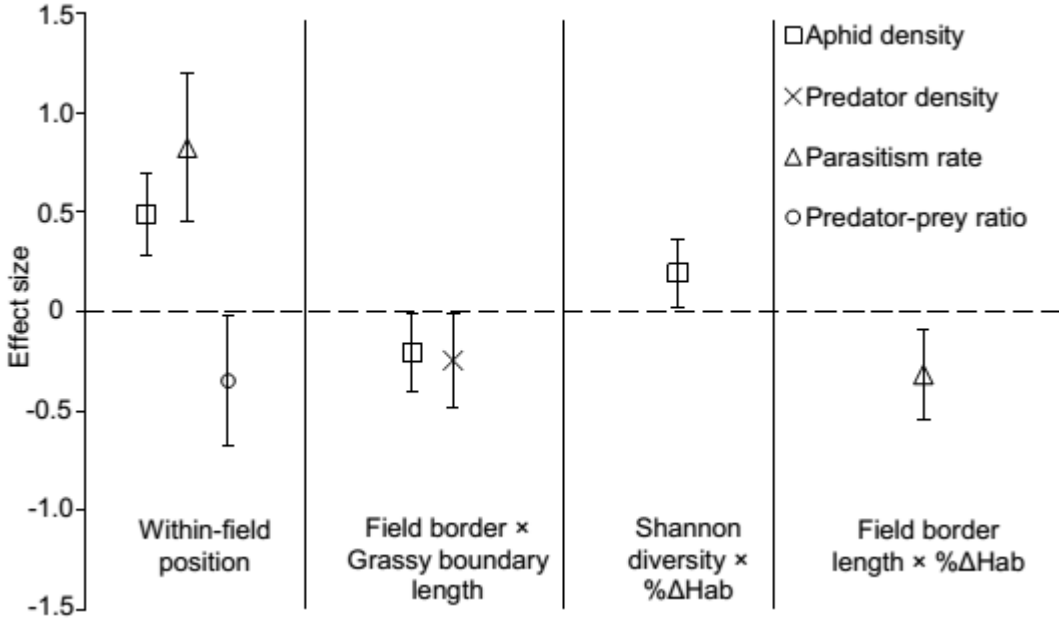


Fig. 1. Effect sizes (multimodel estimate ± 95% confidence interval) of best models (ΔAIC < 2) relating aphid density, predator density, predator to prey ratio and parasitism to fixed effect variables. Response and explanatory variables are standardized (mean centred and scaled), except for predator density and parasitism rate which were fitted with poisson and binomial error distributions. Only significant variables are presented ($P < 0{\cdot}05$). Effect sizes for within-field position are indicative for border and field interior at 10m. Estimates of interaction terms represent the direction of change in slope when variable values increase (see Figs 3& 4). See Table S3 for a more detailed statistical summary.

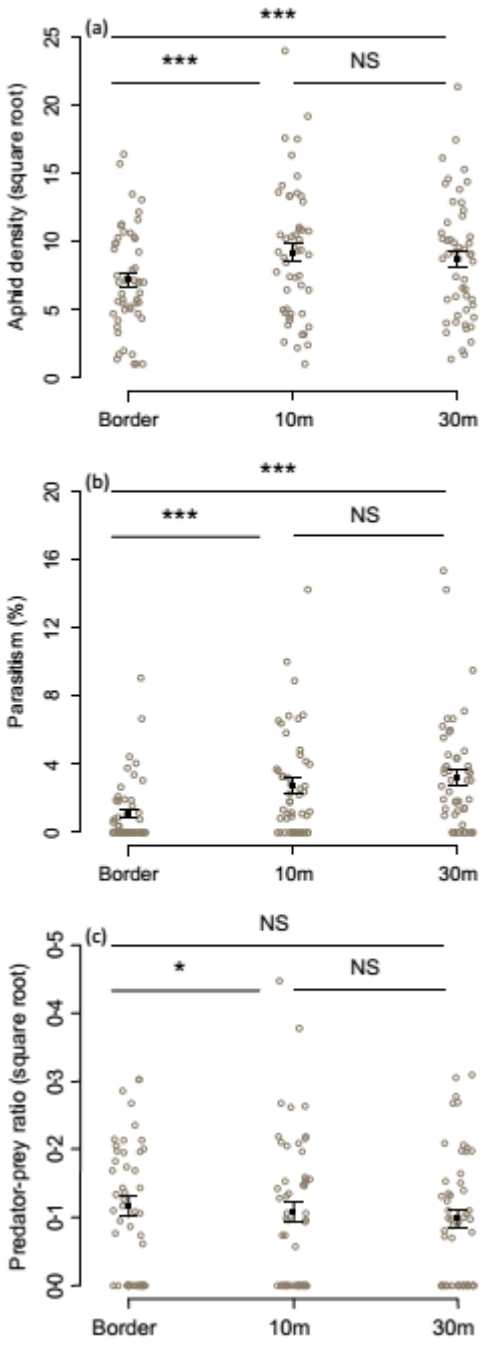


Fig. 2. Effect of the within-field position at the first wheat field row (Border) and at the field interior (10 m and 30 m from field border) on the average aphid density (a), parasitism rate (b) and predator-prey ratio (c). Values are in unit per 60 wheat shoots. Plain squares are mean and error bars represent standard errors. Intra-group statistical significance are shown by stars (*0·01< P < 0·05; ***P < 0·001) and NS (not significant, P > 0·05).

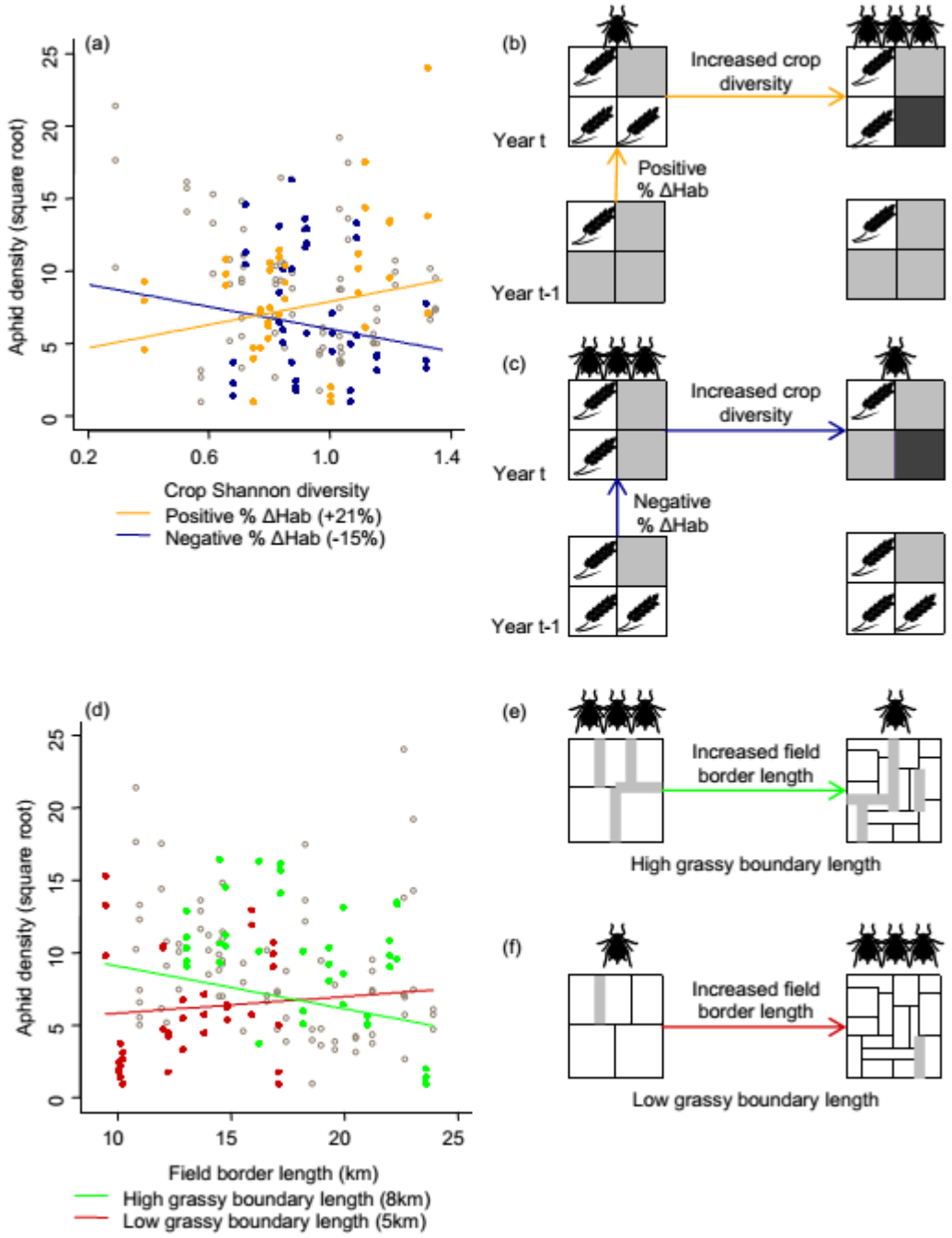


Fig. 3. Aphid density response to interacting effects of (a) crop Shannon diversity (SHDI) conditioned on inter-annual change in aphid habitat cover (% ΔHab). Representation of aphid density (b) increase with SHDI and positive % ΔHab and (c) decrease with crop diversity and negative % ΔHab. Large squares are landscapes and colours represent different crops. Cereal spikes symbolise aphid habitats. Aphid density response to interacting effects of (d) field border length (FBL) conditioned on grassy boundary length (GBL). Representation of aphid density (e) decrease with FBL and high GBL and (f) increase with FBL and low GBL. Black lines within large squares represent field borders and large grey lines represent grassy boundaries.
Lines show model predictions. For illustrative purpose data points are classified into (a) negative (blue; -36 to -10%), intermediate (open dots; -10 to +15%) and positive (yellow; +15 to 43%) % ΔHab values and (d) low (red; 3 to 5 km), intermediate (open dots; 5 to 8 km) and high (blue; 8 to 12 km) GBL values. See Table S3 for a more detailed statistical summary.

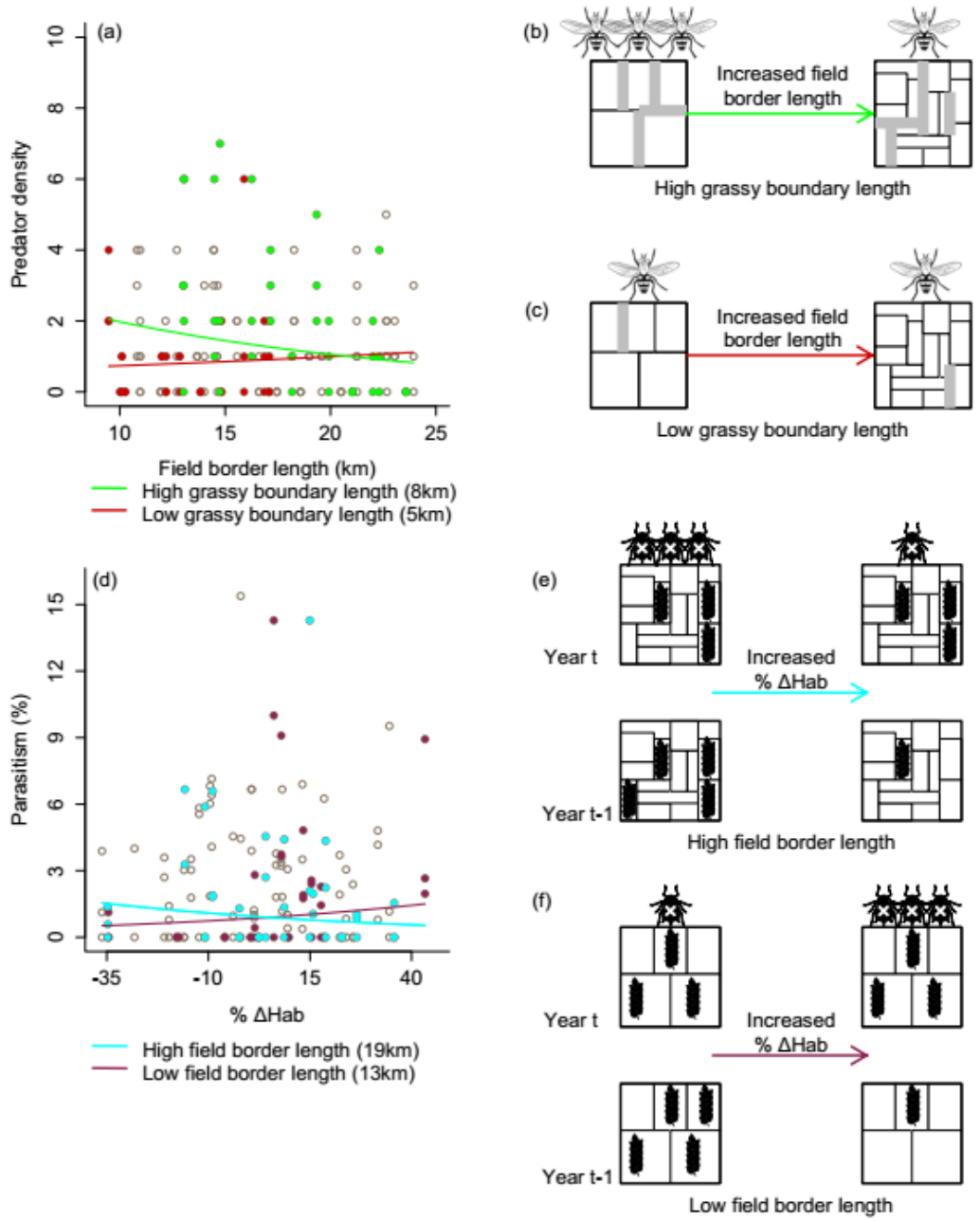


Fig. 4. Vegetation-dwelling predator density response to interacting effect of (a) field border length (FBL) conditioned on grassy boundary length (GBL). Representation of predator density (b) decrease with FBL and high GBL and (c) increase with FBL and low GBL. Black lines within large squares represent field borders and large grey lines represent grassy boundaries. Parasitism rate response to interacting effect of (d) inter-annual change in aphid habitat cover (% ΔHab) conditioned on FBL. Representation of parasitism rate (e) decrease with % ΔHab and high FBL and (f) increase with % ΔHab and low FBL. Crossed out aphids symbolise parasitized aphids and cereal spikes symbolise aphid habitats.
Lines show model predictions. For illustrative purpose data points in (a) are classified in the same way as in Fig. 3d and are classified in (b) into low (purple; 9 to 13 km), intermediate (open dots; 13 to 19 km) and positive (blue; 19 to 24 km) FBL values. See Table S3 for a more detailed statistical summary.

Discussion

This study shows that aphid densities are less abundant close to field borders and decreased with (a) increasing crop diversity when inter-annual change in aphid habitat cover was negative and with (b) increasing field border length when grassy boundaries were high. Moreover, vegetation-dwelling predators followed the same trend as aphid densities, decreasing with increasing field border length when grassy boundaries were high. Aphid parasitism rates increased with increasing inter-annual change in aphid host habitat in large field landscapes.

Local scale effects

As hypothesised, we found that (a) aphid densities were lower at the field border and (b) predator-prey ratios were higher at the field border than further into the field. In contradiction with our hypothesis, (a) parasitism rates were lower at the field border than further into the field and (b) predator densities were not affected by the within field transect position. Several studies reported that aphid densities, predator densities and predator-prey ratios are higher at field borders than field interiors suggesting that field margins can act as source of aphids, predators and parasitoids colonising fields (Krauss, Gallenberger & Steffan-Dewenter 2011; Al Hassan *et al.* 2013; Zhao *et al.* 2013b; Plećaš *et al.* 2014). However, some other authors found in accordance with our results more aphids within fields than at the border (Fievet *et al.* 2007; Caballero-López *et al.* 2012). Within-field aphid populations are dynamic and redistribute quickly temporally and spatially in cereal fields (Winder *et al.* 2005) partly due to their transient nature (Fievet *et al.* 2007). Vialatte *et al.* (2007), studying the genetic structure of aphids collected in uncultivated habitats and cereal fields, found that populations from adjacent field margins are weakly related to aphids colonising fields. This suggests that aphids present in fields are not necessarily spilling-over from the adjacent field margins, but may colonise from semi-natural habitats further away.

Vegetation-dwelling predators were not affected *per se* by the within-field position. However, predator-prey ratios were slightly higher at the field borders (i.e. more predators per aphid) while aphids were less numerous. This suggests that predators may have regulated aphid populations at field borders. Predators and aphid densities were weakly positively correlated (see Table S5), this may be due to aggregation of predators in remaining areas of higher prey density.

Parasitism rates followed a similar pattern as aphid density in the field. This suggests that parasitoids were driven by aphid densities rather than regulating their population (Chaplin-Kramer *et al.* 2011).

Interacting composition and temporal effects

Aphids were affected by crop diversity depending on the inter-annual change in aphid host habitats (% ΔHab; cereal, maize and grasslands). In line with our first hypothesis, aphid densities increased with crop diversity when the cover in suitable habitats increased inter-annually supporting the crowding effect hypothesis (Grez *et al.* 2004).The crop diversity was strongly negatively correlated to the proportion of winter cereal in the landscape (Spearman's rho= - 0·71), which was the main annual aphid host crop available at the time we monitored aphids. Complementary analyses on aphid density response to the cereal cover and % ΔHab interaction showed similar results (P = 0.003). Thus, aphid densities were reduced with increasing cereal cover, supporting the dilution effect. This effect has been reported in other pest systems as well (e.g. Schneider *et al.* 2015). However, dilution effect was observed only when the cover in aphid habitats was lower in the previous year (positive % ΔHab). The effect was reversed with a negative % ΔHab, not supporting the dilution and crowding effect hypothesis. Interestingly % ΔHab was not related to crop diversity, but it was positively correlated to the winter cereal cover. This means that landscapes with low cereal cover (high crop diversity) had as well higher aphid habitats cover compared to the previous year. A possible explanation is that in diversified landscapes, the increase in crop diversity reduced cereal cover such that large aphid population could not be supported anymore (Fahrig 2003). These results emphasize the beneficial effect of crop diversification, especially in landscapes where cereal cover has been reduced compared to the year before.

Interacting configuration and temporal effects

Effects of increased field border length (i.e. landscapes with smaller fields) on aphid and vegetation-dwelling predator densities were dependent on the density of grassy boundaries. As hypothesised, aphid densities decreased with field border length (smaller field landscapes) in landscape with high grassy boundary density. Pests with high reproduction rates (such as aphids) may increase in larger host-crop fields through rapid colonization of field interiors (Segoli & Rosenheim 2012). This may be in line with our finding that aphid densities were higher in field interiors than at field borders. This effect could scale up to higher aphid densities in landscapes with larger mean field size, whenever this also applies to fields containing aphid host plants. Indeed, overall mean field size (decreasing field border length) was positively related to mean field size of cereals (Spearman's rho= 0·74).

The evidence that aphid densities decreased only in landscapes with high grassy field boundary length may be related to easier access to fields by predators. Grassy field boundaries are relatively stable habitats in agricultural landscapes, as they offer shelter, alternative food sources and overwintering places for natural enemies (e.g. Ramsden *et al.* 2015). Many specialised aphid predators such as *Syrphidae* and generalists predators such as *Araneae* and other ground-dwelling predators are more abundant close to vegetated field boundaries (Dennis, Fry & Andersen 2000; Pfiffner & Wyss 2004). At a landscape scale, positive effects of grassy boundaries were reported as well (e.g. Haenke *et al.* 2009). However, vegetation-dwelling predators followed the same pattern as aphids suggesting that predator densities were only driven by aphid densities and may not have affected aphid population regulation (Chaplin-Kramer *et al.* 2011). Generalist enemies however, have been shown to effectively regulate aphids (Schmidt *et al.* 2003) and are positively affected by semi-natural habitat in the landscape (Chaplin-Kramer *et al.* 2011). More grassy boundaries in smaller field landscapes may increase the interface between grassy field boundaries and crops (Fahrig *et al.* 2011). This may have facilitated spill-over of predators into crops (Blitzer *et al.* 2012) and contributed to reducing aphid densities.

However, the negative effect of field border length on aphids was reversed when grassy field boundaries length was lower. If we assume that grassy boundaries support natural enemies of aphids as discussed above, it is not surprising that a negative trend occurred when grassy boundary length was low. Low density of grassy field boundaries may have impeded the spill-over of natural enemies into fields. Thus, low grassy boundaries density may have counteracted the effect of decreased field size in the landscape.

Parasitism rates were affected by inter-annual change in aphid host habitats depending on the field border length. Parasitism decreased with increasing inter-annual aphid habitat cover in landscape with high field border length (i.e. landscapes with smaller fields), supporting the dilution effect hypothesis. A dilution effect on cereal aphid parasitism related to inter-annual increase of cereal cover was also supported by Zhao *et al.* (2013a). Parasitoids are usually poor dispersers (Thies, Roschewitz & Tscharntke 2005). However, landscape with smaller fields may facilitate parasitoid movement when distances between fields are lower. Moreover, some parasitoid species are polyphagous (Kavallieratos *et al.* 2004), and may parasitize aphids present in other crops. Landscapes with smaller fields may therefore facilitate the spill-over between different crops (Fahrig *et al.* 2011). This resulted in locally lower parasitism rates in smaller field landscapes when the inter-annual aphid cover increases. In contrast, parasitism rates increased with the expansion of aphid habitat cover between years in landscapes with low field border length (i.e. landscape with larger fields). This result did not support the dilution-crowding effect hypothesis. In larger field landscapes, the distance between fields hosting aphids in successive years may increase due to crop rotation (Thies, Steffan-Dewenter & Tscharntke 2008). Parasitoids movements may be impaired by large distances between fields, since they are poor dispersers. This is more likely to happen in large field landscapes with decreasing aphid habitat cover between two successive years. As a result, parasitism concentrated locally when the inter-annual change in aphid habitat was positive. This effect supports the concentration hypothesis (Root 1973).

Conclusion and management implications

Our most important finding was that cereal aphid densities were affected by composition and configuration in combination with temporal heterogeneity of crops in the landscape. First, we found that increasing crop diversity and inter-annually decreasing host crop (cereal, maize, grasslands) cover reduced aphid densities. This effect is working in two dimensions (space and time), emphasizing the importance of crop rotations (Rusch *et al.* 2010). In landscape dominated by cereals, we suggest that these crops should be more rotated in space in order to avoid aggregation of large cereal patches in the landscapes. Other crops than cereal could be interspersed within cereal-maize dominated landscapes. Such a measure may be more easily achieved in small-field landscapes as they contain more fields per unit area. Second, high amounts of grassy field boundaries in combination with smaller fields in the landscape can help reducing aphid densities. This finding calls for the maintenance of small-sized farms, which have been shown to have smaller fields on average (Levin 2006). In conclusion, cereal pest reduction can be achieved by changes in crop composition and configuration. Promoting small-scale landscapes and maintaining field boundary vegetation as well as optimizing rotations can contribute to pest control even in landscapes dominated by intensively cultivated land.

Acknowledgements

We thank the farmers for field work allowance. The Agricultural Ministry of Lower Saxony is thanked for providing land use data. A special thank goes to Annika Haß for help in the fields and valuable comments on the manuscript. A.B.B. was supported by a scholarship from the German Academic Exchange Service (DAAD), P.B. by the German Research Foundation (DFG BA 4438/1-2). The study was performed within the ERA-Net BiodivERsA project "FarmLand" financed by the Federal Ministry of Education and Research (BMBF).

References

Al Hassan, D., Georgelin, E., Delattre, T., Burel, F., Plantegenest, M., Kindlmann, P. & Butet, A. (2013) Does the presence of grassy strips and landscape grain affect the spatial distribution of aphids and their carabid predators? *Agricultural and Forest Entomology*, **15**, 24–33.

Barton, K. (2016) MuMIn: Multi-Model Inference. R package version 1.15.6., https://CRAN.R-project.org/package=MuMIn

Bates, D., Mächler, M., Bolker, B. & Walker, S. (2015) Fitting Linear Mixed-Effects Models using lme4. *Journal of Statistical Software*, **67**, 1–48.

Bertrand, C., Burel, F. & Baudry, J. (2016) Spatial and temporal heterogeneity of the crop mosaic influences carabid beetles in agricultural landscapes. *Landscape Ecology*, **31**, 451–466.

Bianchi, F.J.J.A., Booij, C.J.H. & Tscharntke, T. (2006) Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. *Proceedings of the Royal Society of London B: Biological Sciences*, **273**, 1715–1727.

Blitzer, E.J., Dormann, C.F., Holzschuh, A., Klein, A.-M., Rand, T.A. & Tscharntke, T. (2012) Spillover of functionally important organisms between managed and natural habitats. *Agriculture, Ecosystems & Environment*, **146**, 34–43.

Bommarco, R., Kleijn, D. & Potts, S.G. (2013) Ecological intensification: harnessing ecosystem services for food security. *Trends in Ecology & Evolution*, **28**, 230–238.

Burnham, K.P. & Anderson, D.R. (2004) Multimodel Inference: Understanding AIC and BIC in Model Selection. *Sociological Methods & Research*, **33**, 261–304.

Caballero-López, B., Bommarco, R., Blanco-Moreno, J.M., Sans, F.X., Pujade-Villar, J., Rundlöf, M. & Smith, H.G. (2012) Aphids and their natural enemies are differently affected by habitat features at local and landscape scales. *Biological Control*, **63**, 222–229.

Chaplin-Kramer, R., O'Rourke, M.E., Blitzer, E.J. & Kremen, C. (2011) A meta-analysis of crop pest and natural enemy response to landscape complexity. *Ecology Letters*, **14**, 922–932.

Dennis, P., Fry, G.L.A. & Andersen, A. (2000) The Impact of Field Boundary Habitats on the Diversity and Abundance of Natural Enemies in Cereals. *Interchanges of Insects between Agricultural and Surrounding Landscapes* (eds B. Ekbom, M.E. Irwin, & Y. Robert), pp. 195–214. Springer Netherlands, Dordrecht.

Fahrig, L. (2003) Effects of Habitat Fragmentation on Biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, **34**, 487–515.

Fahrig, L., Baudry, J., Brotons, L., Burel, F.G., Crist, T.O., Fuller, R.J., Sirami, C., Siriwardena, G.M. & Martin, J.-L. (2011) Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecology Letters*, **14**, 101–112.

Fahrig, L., Girard, J., Duro, D., Pasher, J., Smith, A., Javorek, S., King, D., Lindsay, K.F., Mitchell, S. & Tischendorf, L. (2015) Farmlands with smaller crop fields have higher within-field biodiversity. *Agriculture, Ecosystems & Environment*, **200**, 219–234.

Fievet, V., Dedryver, C.-A., Plantegenest, M., Simon, J.-C. & Outreman, Y. (2007) Aphid colony turn-over influences the spatial distribution of the grain aphid Sitobion avenae over the wheat growing season. *Agricultural and Forest Entomology*, **9**, 125–134.

Finch, S. & Collier, R. h. (2000) Host-plant selection by insects – a theory based on 'appropriate/inappropriate landings' by pest insects of cruciferous plants. *Entomologia Experimentalis et Applicata*, **96**, 91–102.

Firbank, L.G., Petit, S., Smart, S., Blain, A. & Fuller, R.J. (2008) Assessing the impacts of agricultural intensification on biodiversity: a British perspective. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **363**, 777–787.

Geiger, F., Bengtsson, J., Berendse, F., Weisser, W.W., Emmerson, M., Morales, M.B., Ceryngier, P., Liira, J., Tscharntke, T., Winqvist, C., Eggers, S., Bommarco, R., Pärt, T., Bretagnolle, V., Plantegenest, M., Clement, L.W., Dennis, C., Palmer, C., Oñate, J.J., Guerrero, I., Hawro, V., Aavik, T., Thies, C., Flohre, A., Hänke, S., Fischer, C., Goedhart, P.W. & Inchausti, P. (2010) Persistent negative effects of pesticides on biodiversity and biological control potential on European farmland. *Basic and Applied Ecology*, **11**, 97–105.

Grez, A., Zaviezo, T., Tischendorf, L. & Fahrig, L. (2004) A Transient, Positive Effect of Habitat Fragmentation on Insect Population Densities. *Oecologia*, **141**, 444–451.

Haenke, S., Scheid, B., Schaefer, M., Tscharntke, T. & Thies, C. (2009) Increasing syrphid fly diversity and density in sown flower strips within simple vs. complex landscapes. *Journal of Applied Ecology*, **46**, 1106–1114.

Hand, S.C. (1989) The overwintering of cereal aphids on Gramineae in southern England, 1977–1980. *Annals of Applied Biology*, **115**, 17–29.

Jonsson, M., Wratten, S.D., Landis, D.A. & Gurr, G.M. (2008) Recent advances in conservation biological control of arthropods by arthropods. *Biological Control*, **45**, 172–175.

Kavallieratos, N.G., Tomanović, Ž., Starý, P., Athanassiou, C.G., Sarlis, G.P., Petrović, O., Niketić, M. & Veroniki, M.A. (2004) A survey of aphid parasitoids (Hymenoptera: Braconidae: Aphidiinae) of Southeastern Europe and their aphid-plant associations. *Applied Entomology and Zoology*, **39**, 527–563.

Krauss, J., Gallenberger, I. & Steffan-Dewenter, I. (2011) Decreased Functional Diversity and Biological Pest Control in Conventional Compared to Organic Crop Fields ed A. Hector. *PLoS ONE*, **6**, e19502.

Leather, S.R. (1993) Overwintering in six arable aphid pests: a review with particular relevance to pest management. *Journal of Applied Entomology*, **116**, 217–233.

Levin, G. (2006) Farm size and landscape composition in relation to landscape changes in Denmark. *Geografisk Tidsskrift-Danish Journal of Geography*, **106**, 45–59.

Östman, Ö., Ekbom, B. & Bengtsson, J. (2001) Landscape heterogeneity and farming practice influence biological control. *Basic and Applied Ecology*, **2**, 365–371.

Palmu, E., Ekroos, J., Hanson, H.I., Smith, H.G. & Hedlund, K. (2014) Landscape-scale crop diversity interacts with local management to determine ground beetle diversity. *Basic and Applied Ecology*, **15**, 241–249.

Pasher, J., Mitchell, S.W., King, D.J., Fahrig, L., Smith, A.C. & Lindsay, K.E. (2013) Optimizing landscape selection for estimating relative effects of landscape variables on ecological responses. *Landscape Ecology*, **28**, 371–383.

Pimentel, D. (2005) Environmental and economic costs of the application of pesticides primarily in the United States. *Environment, Development and Sustainability*, **7**, 229–252.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Core Team. (2016) nlme: Linear and Nonlinear Mixed Effects Models, http://cran.r-project.org/web/packages/nlme/

Plećaš, M., Gagić, V., Janković, M., Petrović-Obradović, O., Kavallieratos, N.G., Tomanović, Ž., Thies, C., Tscharntke, T. & Ćetković, A. (2014) Landscape composition and configuration influence cereal aphid–parasitoid–hyperparasitoid interactions and biological control differentially across years. *Agriculture, Ecosystems and Environment*, **183**, 1–10.

Ramsden, M.W., Menéndez, R., Leather, S.R. & Wäckers, F. (2015) Optimizing field margins for biocontrol services: The relative role of aphid abundance, annual floral resources, and overwinter habitat in enhancing aphid natural enemies. *Agriculture, Ecosystems & Environment*, **199**, 94–104.

R Core Team. (2015) R: A language and environment for statistical computing, https://www.R-project.org/

Ricci, B., Franck, P., Toubon, J.-F., Bouvier, J.-C., Sauphanor, B. & Lavigne, C. (2009) The influence of landscape on insect pest dynamics: a case study in southeastern France. *Landscape Ecology*, **24**, 337–349.

Root, R.B. (1973) Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (Brassica Oleracea). *Ecological Monographs*, **43**, 95.

Rusch, A., Valantin-Morison, M., Sarthou, J.-P. & Roger-Estrade, J. (2010) Biological Control of Insect Pests in Agroecosystems: Effects of Crop Management, Farming Systems, and Seminatural Habitats at the Landscape Scale: A Review. *Advances in Agronomy* (ed D.L. Sparks), pp. 219–259. Academic Press.

Schellhorn, N.A., Gagic, V. & Bommarco, R. (2015) Time will tell: resource continuity bolsters ecosystem services. *Trends in Ecology & Evolution*, **30**, 524–530.

Schmidt, M.H., Lauer, A., Purtauf, T., Thies, C., Schaefer, M. & Tscharntke, T. (2003) Relative importance of predators and parasitoids for cereal aphid control. *Proceedings of the Royal Society B: Biological Sciences*, **270**, 1905–1909.

Schneider, G., Krauss, J., Riedinger, V., Holzschuh, A. & Steffan-Dewenter, I. (2015) Biological pest control and yields depend on spatial and temporal crop cover dynamics ed P. Manning. *Journal of Applied Ecology*, **52**, 1283–1292.

Segoli, M. & Rosenheim, J.A. (2012) Should increasing the field size of monocultural crops be expected to exacerbate pest damage? *Agriculture, Ecosystems & Environment*, **150**, 38–44.

Steinmann, H.-H. & Dobers, E.S. (2013) Spatio-temporal analysis of crop rotations and crop sequence patterns in Northern Germany: potential implications on plant health and crop protection. *Journal of Plant Diseases and Protection*, **120**, 85–94.

Thies, C., Roschewitz, I. & Tscharntke, T. (2005) The landscape context of cereal aphid-parasitoid interactions. *Proceedings of the Royal Society B: Biological Sciences*, **272**, 203–210.

Thies, C., Steffan-Dewenter, I. & Tscharntke, T. (2008) Interannual landscape changes influence plant–herbivore–parasitoid interactions. *Agriculture, Ecosystems & Environment*, **125**, 266–268.

Tscharntke, T., Tylianakis, J.M., Rand, T.A., Didham, R.K., Fahrig, L., Batáry, P., Bengtsson, J., Clough, Y., Crist, T.O., Dormann, C.F., Ewers, R.M., Fründ, J., Holt, R.D., Holzschuh, A., Klein, A.M., Kleijn, D., Kremen, C., Landis, D.A., Laurance, W., Lindenmayer, D., Scherber, C., Sodhi, N., Steffan-Dewenter, I., Thies, C., van der Putten, W.H. & Westphal, C. (2012) Landscape moderation of biodiversity patterns and processes - eight hypotheses. *Biological Reviews*, **87**, 661–685.

Vasseur, C., Joannon, A., Aviron, S., Burel, F., Meynard, J.-M. & Baudry, J. (2013) The cropping systems mosaic: How does the hidden heterogeneity of agricultural landscapes drive arthropod populations? *Agriculture, Ecosystems & Environment*, **166**, 3–14.

Veres, A., Petit, S., Conord, C. & Lavigne, C. (2013) Does landscape composition affect pest abundance and their control by natural enemies? A review. *Agriculture, Ecosystems & Environment*, **166**, 110–117.

Vialatte, A., Plantegenest, M., Simon, J.-C. & Dedryver, C.-A. (2007) Farm-scale assessment of movement patterns and colonization dynamics of the grain aphid in arable crops and hedgerows. *Agricultural and Forest Entomology*, **9**, 337–346.

Vialatte, A., Simon, J.-C., Dedryver, C.-A., Fabre, F. & Plantegenest, M. (2006) Tracing individual movements of aphids reveals preferential routes of population transfers in agroecosystems. *Ecological Applications*, **16**, 839–844.

Winder, L., Griffiths, G.J.K., Perry, J.N., Alexander, C.J., Holland, J.M., Kennedy, P.J. & Birt, A. (2005) The role of large-scale spatially explicit and small-scale localized processes on the population dynamics of cereal aphids. *Bulletin of Entomological Research*, **95**, 579–587.

Zhao, Z.-H., Hui, C., He, D.-H. & Ge, F. (2013a) Effects of position within wheat field and adjacent habitats on the density and diversity of cereal aphids and their natural enemies. *BioControl*, **58**, 765–776.

Zhao, Z.-H., Hui, C., Ouyang, F., Liu, J.-H., Guan, X.-Q., He, D.-H. & Ge, F. (2013b) Effects of inter-annual landscape change on interactions between cereal aphids and their natural enemies. *Basic and Applied Ecology*, **14**, 472–479.

Zuur, A.F., Ieno, E.N., Walker, N., Saveliev, A.A. & Smith, G.M. (2009) *Mixed Effects Models and Extensions in Ecology with R*. Springer New York, New York, NY.

Supporting Information

Additional Supporting Information may be found in the online version of this article.
Fig. S1. Map of the study region and design
Table S1. Statistical summary of landscape metrics
Table S2. Correlations between landscape metrics
Table S3. Most parsimonious model results
Table S4. Statistical summary of recorded arthropods
Table S5. Correlations between response variables

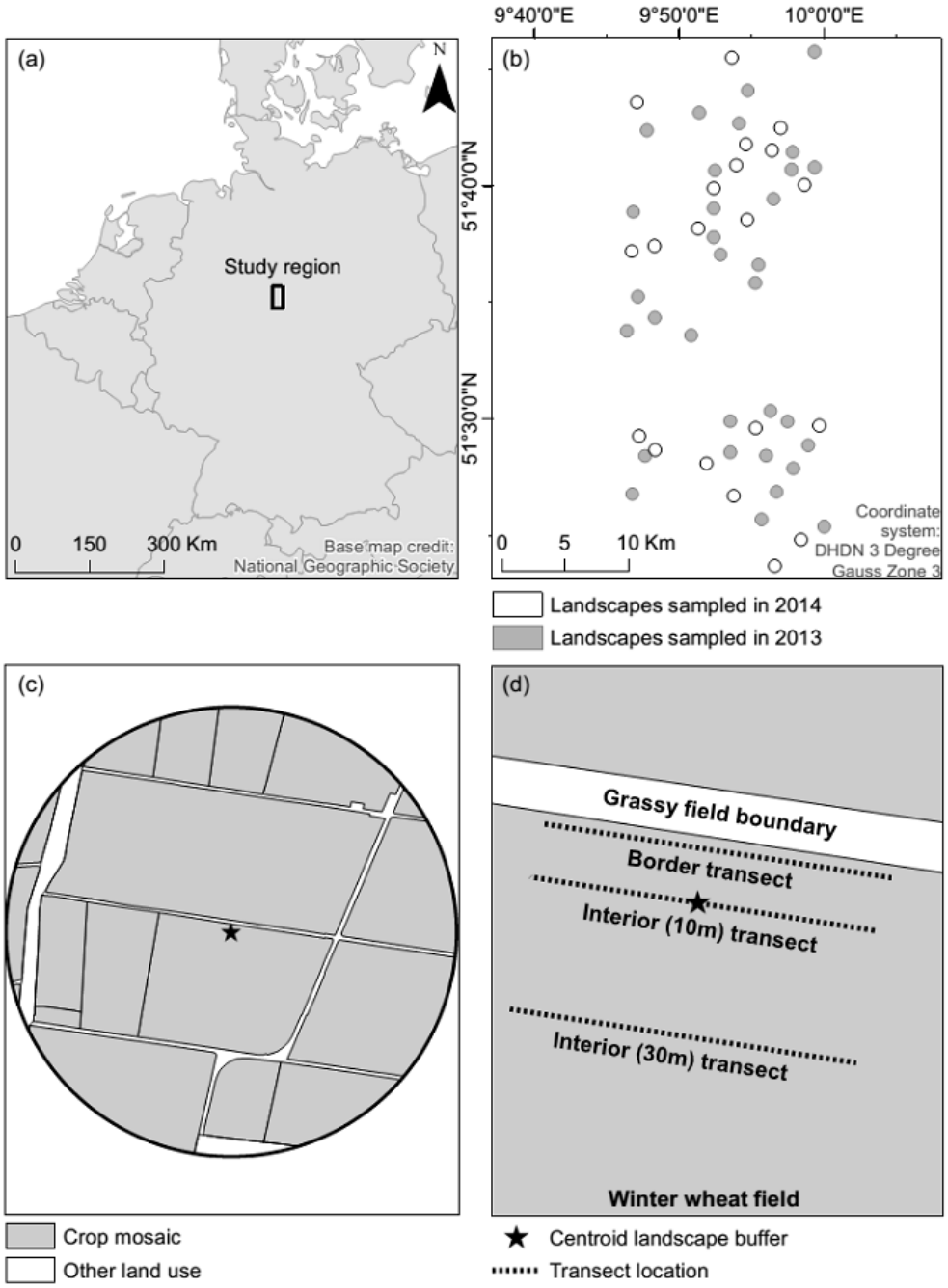


Fig. S1. Map of the study region in central Germany (a) and the distribution of 1km diameter landscape sectors around winter wheat fields sampled in 2013 and 2014 (b). A typical landscape is represented in (c) and the location of the sampled 50m transects (d).

Table S1. Summary statistics of landscape metrics Shannon diversity (SHDI), inter-annual change in aphid habitat cover (% ΔHab), field border length (FBL), grassy boundary length (GBL) and crop cover measured within 1 km diameter sectors around sampled wheat fields.

	Mean ± SEM*	Value range	
		Minimum	Maximum
Landscape variables used for analysis			
SHDI	0·91 ± 0·02	0·29	1·35
% ΔHab (%)	2·90 ± 1·51	- 36·18	43·29
FBL (km)	16·25 ± 0·33	9·47	23·94
GBL (km)	7·09 ± 0·15	3·39	11·50
Other landscape metric			
Crop cover (%)	85·37 ± 0·64	66·98	96·00

*SEM= Standard error of mean

Table S2. Spearman rank correlation coefficients (Spearman's rho) between landscape variables crop Shannon diversity (SHDI), inter-annual change in aphid habitat cover (% ΔHab), field border length in km (FBL) and grassy boundary length in km (GBL) within 1km diameter landscape sector around sampled wheat fields.

	SHDI	% ΔHab	FBL	GBL
SHDI	1	- 0·25	0·38	- 0·02
% ΔHab (%)	- 0·25	1	0·14	0·14
FBL (km)	0·38	0·14	1	0·40
GBL (km)	- 0·02	0·14	0·40	1

Spearman correlations $|rho| \leq 0{\cdot}39$, 0·4 - 0·59, $\geq 0{\cdot}6$ are considered respectively as weak, moderate and strong (Campbell & Swinscow 2009)

Campbell, M.J. & Swinscow, T.D.V. (2009) *Statistics at Square One*, 11th Edition. Wiley-Blackwell, Chichester, West Sussex.

Table S3. Results of the best models relating aphid density (square root transformed), predator density, predator-prey ratio (square root transformed) and parasitism rate to explanatory variables. All variables present in the best models (ΔAIC < 2) are presented; significant *P* values are in bold characters. Densities are numbers per 60 shoots. *n* is the number of statistical units (transects) analysed. Within-field position represents the position of transects at the field border, 10m and 30m from the field border. All explanatory variables are standardised (mean-centred and scaled by standard deviation).

Fixed effect variable	*P*	Standardised model estimate ± 95% confidence interval (CI)
Aphid density * (*n* = 153)		
Within-field position (Border – 10m)	< 0·001	0·50 ± 0·21
Within-field position (Border – 30m)	< 0·001	0·38 ± 0·21
Within-field position (10m – 30m)	0·265	-0·12 ± 0·21
Crop Shannon diversity	0·994	0·01 ± 0·16
Field border length	0·300	-0·10 ± 0·18
Grassy boundary length	0·224	0·13 ± 0·20
Change in aphid habitat	0·132	0·12 ± 0·15
Field border length × Grassy boundary length	0·041	-0·21 ± 0·20
Field border length × % ΔHab	0·417	0·08 ± 0·18
Crop Shannon diversity × Field border length	0·079	0·13 ± 0·15
Crop Shannon diversity × % ΔHab **	0·032	0·20 ± 0·18
Vegetation-dwelling predator density (*n* = 153)		
Within-field position (Border – 10m)	0·061	0·32 ± 0·33
Within-field position (Border – 30m)	0·287	0·19 ± 0·34
Within-field position (10m – 30m)	0·412	-0·14 ± 0·32
Crop Shannon diversity	0·355	-0·10 ± 0·20
% ΔHab	0·518	0·06 ± 0·19
Field border length	0·523	-0·08 ± 0·24
Grassy boundary length	0·039	0·27 ± 0·25
Field border length × Grassy boundary length	0·042	-0·25 ± 0·24
Crop Shannon diversity × Field border length	0·097	0·16 ± 0·19
Predator to prey ratio * (*n* = 152)		
Within-field position (Border – 10m)	0·043	-0·35 ± 0·34
Within-field position (Border – 30m)	0·065	-0·32 ± 0·34
Within-field position (10m – 30m)	0·855	0·04 ± 0·34
Crop Shannon diversity	0·336	-0·15 ± 0·29
Grassy boundary length	0·207	0·14 ± 0·21

Table S3. (continued)

Fixed effect variable	*P*	Standardised model estimate ± 95% confidence interval (CI)
Parasitism rate (*n* =149)		
Within-field position (Border – 10m)	< 0·001	0·83 ± 0·37
Within-field position (Border – 30m)	< 0·001	0·87 ± 0·37
Within-field position (10m – 30m)	0·747	0·05 ± 0·26
Field border length	0·818	0·03 ± 0·20
Change in aphid habitat	0·905	-0·02 ± 0·18
Field border length × % ΔHab	0·008	-0·32 ± 0·23

* Standardised response (mean-centered and scaled by standard deviation)
** % ΔHab is the inter-annual change in aphid habitat cover.

Table S4. Summary statistics of arthropods monitored on a total of 9360 wheat shoots in 51 fields. Data are pooled over two wheat phenological stages (wheat flowering and milk ripening periods) and pooled within three sampling field-locations (Field border· field interior at 10m and field interior at 30m). Means and value ranges are presented as units per 60 wheat shoots (30 shoots × 2 phenological stages). Only aphid density· predator density· predator to prey ratio and parasitism proportion are analysed as response variables.

	Mean ± SEM*	Value range	
		Minimum	Maximum
Aphid density (all species)	89·25 ± 7·32	1	577
Sitobion avenae density	68·60 ± 5·62	0	405
Metopolophium dirhodum density	18·01 ± 1·94	0	120
Rhopalosiphum padi density	0·05 ± 0·03	0	3
Mummified aphid density	2·59 ± 0·68	0	102
Predator density (all taxa)	1·38 ± 0·13	0	7
Syrphidae larvae density	0·72 ± 0·01	0	6
Araneae (*Linyphiidae*) density	0·47 ± 0·07	0	6
Chrysopidae larvae density	0·12 ± 0·03	0	3
Coccinellidae adults and larvae density	0·02 ± 0·01	0	1
Predator-prey ratio**	0·03 ± 0·01	0	1
Parasitism rate (%)***	3·00 ± 3·00	0	33

* SEM= Standard error of mean
** Predator-prey ratio calculated as [Predator density/ Aphid density]
*** Parasitism rate calculated as [(Mummified aphid density/ Aphid density)× 100]

Table S5. Spearman rank correlation coefficients (Spearman's rho) between response variables aphid (square root transformed)· predator densities· parasitism rates and predator-prey ratios (square root transformed). Variable pairs are considered strongly correlated when |rho| > 0·6 (Campbell & Swinscow 2009).

	Aphid density	Predator density	Predator to prey ratio	Parasitism rates
Aphid density	1	0·5	- 0·1	- 0·2
Predator density	0·5	1	0·8	- 0·2
Predator to prey ratio	- 0·1	0·8	1	0·1
Parasitism rates	- 0·2	- 0·2	- 0·1	1

Campbell· M.J. & Swinscow· T.D.V. (2009) *Statistics at Square One*· 11th Edition. Wiley-Blackwell· Chichester· West Sussex.

CHAPTER 5
Landscape-wide crop diversity and mean field size affect community body size structure and body size of *Poecilus cupreus*

This chapter presents preliminary results at an early stage of preparation and is thus not written in a publishable journal article style.

Introduction

Carabid beetles can be effective in regulating pest population in fields (Symondson 2002). Promoting these biocontrol agents requires a landscape-perspective (Tscharntke *et al.* 2007). Carabids may be sensitive to the landscape heterogeneity, as they move across several habitats including cultivated fields during their life-time (Bommarco 1998a). For example, carabid species richness was enhanced by crop diversity in the landscape (Palmu *et al.* 2014) and by the decrease in mean field size (Bertrand, Baudry & Burel 2016). Although, the degree to which species richness contribute to pest suppression is not evident and may depend on factors such as species interactions or traits (Straub, Finke & Snyder 2008; Bell *et al.* 2008). As an example, body size of species may affect pest suppression, since larger species need more prey *per capita* and may preferably prey on larger preys as compared to smaller species (Brose *et al.* 2008). In addition, within-species body size and body condition, which relate to fitness, may affect the persistence of carabid populations in landscapes. Better body condition revealing feeding status of carabids, has been demonstrated to correlate with enhanced reproduction ability in some species (Bommarco 1998a). First studies on carabid condition suggested that small-field landscapes and high crop diversity had positive effects on carabid beetles fecundity and body condition (Bommarco 1998a; Östman *et al.* 2001).
In this study, we assess in parallel the effect of landscape-wide crop diversity and mean field size on community weighted mean body size (dominant body size in communities), mean body size and body condition of three common carabid beetles in cereal and oilseed rape: *Anchomenus dorsalis*, *Poecilus cupreus* and *Pterostichus melanarius*. We expected that (1) community body sizes shift from small to large species and (2) body size and body condition of the three species increase with increasing crop diversity in small-field landscapes, as more and better interspersed habitats may lead to landscape complementation of resources (Fahrig *et al.* 2011).

Material and methods

Study area and landscape parameters

The study was conducted in spring 2013 in a 600 km² area within the districts of Göttingen (51°32'N, 9°54'E) and Northeim (51°42'N, 9°59'E), Lower Saxony, Germany. We selected a total of 32 landscapes of 1×1 km along independent gradients of landscape compositional and configurational heterogeneity of crops. To maximise the gradients length, we chose landscapes with high shares of crop cover (mean ± SE: 86% ± 0,9). Landscapes were dominated by cereals (46%), oilseed rape (13%), maize (9%) and sugar beet (9%) and had an average field size of 4 ha. The Shannon diversity of crop types was used as compositional heterogeneity gradient and field border density as configurational heterogeneity gradient. For calculating the Shannon crop diversity index, we used all crop types, while grouping all cereals together (mostly winter wheat and barley). The field border density was computed as the total length of field borders per unit of crop cover (in km. ha^{-1}). Field border density was representative of the mean field size in the landscape as both metrics were strongly negatively correlated (Pearson's r = -0,87). In addition, we measured the cover of semi-natural habitat in the landscape, which included all vegetated field margins, woodlands and calcareous grasslands. We ensured that none of the landscape metrics were correlated (Pearson's |r| between 0,03 and 0,26). Within each landscape, we selected two winter wheat fields and one oilseed rape field. The crops were managed conventionally, with similar amount of nitrogen applied (200 kg N. ha^{-1}). The fields received several application of herbicides and fungicides. Insecticides were applied once in wheat fields and three times on average in oilseed rape fields.

Carabid beetle community sampling

We sampled carabid beetles in each field using pitfall traps. Two 50m long within-field transects were established running parallel to the adjacent field margin. The first transect was placed 1m from the field margin and the second one 25m inside the field. A pitfall trap was placed at each end of the transects. The traps were filled with a water-salt solution (10g $salt.L^{-1}$) and odourless dish soap to reduce surface tension.

Pitfall traps were open in May and in June for four days. Carabid beetles were collected and stored in 70% ethanol before identification to species level. We pooled carabid beetle data over the both sampling periods for further analysis.

Carabid beetle species description

We studied three particular carabid species which were abundant in the sampled community: *Anchomenus dorsalis*, *Poecilus cupreus* and *Pterostichus melanarius*. These species are preferred carnivores, except *P. cupreus*, which is rather omnivorous (Lindroth 1985). *A. dorsalis* is a small-sized beetle (5-8 mm), *P. cupreus* is medium-sized (9-13 mm) and *P. melanarius* is a large-sized beetle (13-17 mm).

A. dorsalis and *P. cupreus* are spring breeding species, which overwinter as adults in non-crop habitats before returning to the fields in spring (Lee & Landis 2002). *P. melanarius* is an autumn breeding species which overwinters as a larva in the first year and as adult in the two next years of life. *P. melanarius* depends on non-crop area for overwintering (Wallin 1985).

Body size and body condition collection

First we compiled mean body size between male and females of all collected species using literature based data. The information was retrieved from the online database carabids.org (Homburg *et al.* 2014). Then we computed the community weighted mean (CWM) of body size to get the average size (in mm) of the whole community weighted by the carabid beetle numbers caught per field.

Second, we selected randomly 3 males and 3 females of *A. dorsalis*, *P. cupreus* and *P. melanarius* from all oilseed rape fields and one cereal field per landscape. If a field contained less than 3 males and females per species, all specimens were selected. We measured the body size of beetles as the sum of elytra length and pronotum length. Beetles were placed on a grid scale under a binocular connected to a camera (Canon EOS 1200D). We took pictures of the beetles and measured the body size to the nearest 0.001mm using the image treatment software JMicroVision (Roduit 2016). Then we dried the beetles for 72 hours at 60°C and measured the dry weight at the nearest 0,001mg.

Statistical analysis

The objective of the study was to relate inter-species CWM body size, intra-species body size of the three species and their body condition to crop type (wheat and oilseed rape), landscape-wide Shannon crop diversity, field border density and semi-natural habitat cover.

We analysed the data using linear mixed effects models in R software (R Core Team 2015) with the "nlme" package 3.1-125 (Pinheiro *et al.* 2016). We use the landscape identity as a random intercept to account for the spatial structure of the data. Landscape metrics where mean-centred and standardized prior to analysis. We analysed males and females of each of the three species separately since males were significantly smaller than females for *A. dorsalis* ($P < 0.01$). Measured body sizes and dry weights were pooled (averaged) over fields, species and genders. We analysed body condition of beetles with dry weight as response and body size as co-variable to account for the dependence between both variables (see Knapp & Knappová 2013). In addition, the number of beetles captured or measured were added as co-variable to the associated responses, to obtain abundance independent results.

We tested the landscape metrics, crop type and their two-way interactions effect on the different responses. We then used multimodel averaging to obtain robust parameter estimates. The procedure was applied using "MuMIn" package 1.15 (Barton 2016). Model averaging was applied on the model set with $\Delta AICc < 2$ (Burnham & Anderson 2004).

Results

We captured a total of 12 852 carabid beetles of 64 species. Most of the beetles were *A. dorsalis* (31%) and *P. melanarius* (28%). We measured and weighted 379 specimens of *A. dorsalis*, 187 of *P. cupreus* and 325 of *P. melanarius*.

Only the carabid beetle community and the species *P. cupreus* were affected by crop type and landscape-wide crop heterogeneity. Cereal fields contained on average larger beetle species than oilseed rape fields (Fig. 1). In contrast, *P. cupreus* females and males were larger in oilseed rape than in cereal fields. The increase in compositional crop heterogeneity (crop Shannon diversity) was related to the shift of the community towards larger species. In contrast, the increase of configurational crop heterogeneity (smaller field size) induced smaller species in the community. *P. cupreus* females became larger with decreasing field size, however only in cereal fields. In contrast, body condition did not vary with crop type or landscape crop heterogeneity. Semi-natural habitat cover did not affect inter and intra-species body size or body condition.

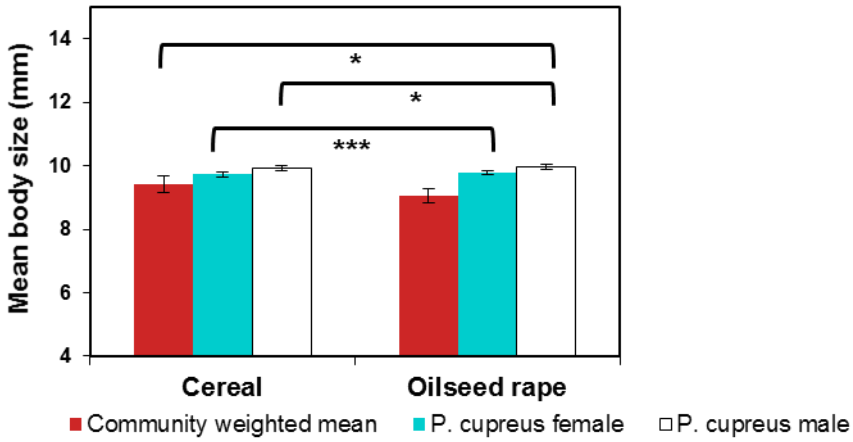


Figure 1. Carabid beetle mean body size of the community and of *P. cupreus* females and males in wheat and oilseed rape fields. * 0,01< P <0,05; *** P < 0,01.

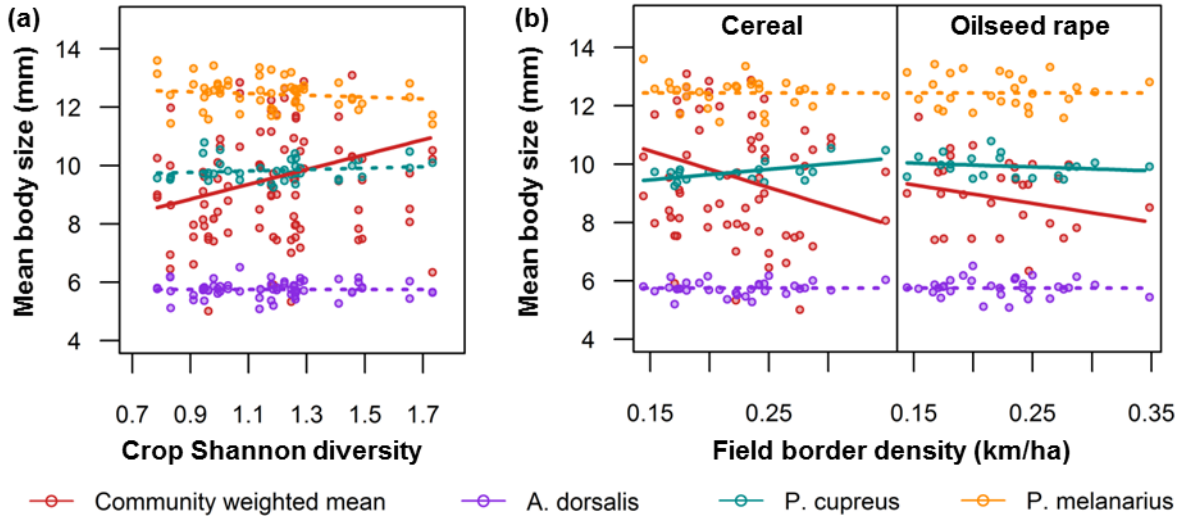


Figure 2. Mean body size of the community and females of *A. dorsalis*, *P.cupreus* and *P. melanarius* in relation to landscape compositional heterogeneity (a) and configurational heterogeneity (b). Only females are represented here, as male body sizes were not significantly related to landscape parameters. Lines are predictions from linear mixed models. Solid lines are significant effects and dashed ones are non-significant.

Discussion

This study demonstrates that landscape-wide compositional and configurational heterogeneity, independently of semi-natural habitats shaped the distribution of body sizes in carabid beetle communities and within the species *P. cupreus*, while body condition of the three species remained unaffected. Crop diversity at the landscape level favoured larger species in the communities, whereas increasing field border density (i.e smaller field size) favoured smaller sized species. Females of the species *P. cupreus* were larger in cereal fields, when field border density increased. More field borders mitigated body sizes in cereal fields which tended to be smaller than in oilseed rape fields.

The shift towards larger carabid species with increasing crop diversity in the landscape suggested that crop diversity associated with more resource availability is beneficial for large species, which are sensitive to management intensity. Large species are more sensitive to disturbance such as pesticides applications than small-sized carabid beetles (Ribera *et al.* 2001; Rusch *et al.* 2013). The average smaller size of species in oilseed rape compared to wheat fields confirmed this idea. Indeed, oilseed rape received more insecticide treatments than wheat fields in our region. At the landscape scale, more diverse crop types may benefit large species by increasing the alternative resources availability and continuity (Fahrig *et al.* 2011; Schellhorn, Gagic & Bommarco 2015).

Large-sized carabid beetle are more sensitive to variability in resource availability as they need more resources during their life-time (Blake *et al.* 1994; Ribera *et al.* 2001). However, it would imply that larger beetles such as *P. melanarius* would have better condition as more food is available in the surrounding landscape. We did not find such effects, neither on the body condition nor on the body size of this species. This suggest that other factors play a role for the feeding in *P. melanarius* such as interactions with other species.

Decreasing average field size in contrast, induced a shift from large to small-sized beetles within the community. Smaller average field size reduce the distance from field edge to interiors and interspersion of habitat is higher in these landscapes (Fahrig *et al.* 2011). This may facilitate dispersal between patches. Especially the smaller carabid species, driven by the most abundant species *A. dorsalis*, were spring breeders. These species overwinter in semi-natural habitats and move to the fields in spring (Holland, Birkett & Southway 2009; Wamser *et al.* 2011), whereas autumn breeding species such as *P. melanarius* can hibernate in fields and may not need to disperse as much as spring breeders (Holland, Birkett & Southway 2009). At the species level, the positive effect of decreasing field size on body size of *P. cupreus*, but not the condition indicated that the configuration of crops in the landscape influenced the larval growth rather than the adult feeding state (reflected by body condition, Bommarco 1998). *P. cupreus* is a spring breeding species, which larvae grow in the field in summer (Bommarco 1998b). This means that the structural body size of sampled individuals reflected the feeding condition of the previous year. This may limit our interpretation. However, since the mean field size do not vary much between years it may well reflect feeding condition in the landscape. Östman *et al.* (2001) found an increase of body condition in *P. cupreus* with higher crop perimeter to area ratio, similar to our field border density measure. They explained this effect by more nearby field margins which are often used as overwintering sites and better access to nearby alternative habitats.

This study showed that increasing landscape-wide crop diversity and decreasing mean field sizes have mixed effects on carabid body size. Increasing the availability of alternative habitats would favour larger species which are more sensitive to management practices. Contrastingly, increasing habitat interspersion may favour small species which often depend on dispersion from semi-natural habitats into crops. Better feeding in small-field landscape may also be revealed by increased body size of *P. cupreus*.

References

Barton, K. (2016) MuMIn: Multi-Model Inference. R package version 1.15.6., https://CRAN.R-project.org/package=MuMIn

Bell, J.R., Mead, A., Skirvin, D.J., Sunderland, K.D., Fenlon, J.S. & Symondson, W.O.C. (2008) Do functional traits improve prediction of predation rates for a disparate group of aphid predators? *Bulletin of Entomological Research*, **98**, 587.

Bertrand, C., Baudry, J. & Burel, F. (2016) Seasonal variation in the effect of landscape structure on ground-dwelling arthropods and biological control potential. *Basic and Applied Ecology*.

Blake, S., Foster, G.N., Eyre, M.D. & Luff, M.L. (1994) Effects of habitat type and grassland management practices on the body size distribution of carabid beetles. *Pedobiologia*, **38**, 502–512.

Bommarco, R. (1998a) Reproduction and Energy Reserves of a Predatory Carabid Beetle Relative to Agroecosystem Complexity. *Ecological Applications*, **8**, 846–853.

Bommarco, R. (1998b) Stage sensitivity to food limitation for a generalist arthropod predator, Pterostichus cupreus. *Environmental Entomology*, **27**, 863–869.

Brose, U., Ehnes, R.B., Rall, B.C., Vucic-Pestic, O., Berlow, E.L. & Scheu, S. (2008) Foraging theory predicts predator–prey energy fluxes - Brose - 2008 - Journal of Animal Ecology - Wiley Online Library. *Journal of Animal Ecology*, **77**, 1072–1078.

Burnham, K.P. & Anderson, D.R. (2004) Multimodel Inference: Understanding AIC and BIC in Model Selection. *Sociological Methods & Research*, **33**, 261–304.

Fahrig, L., Baudry, J., Brotons, L., Burel, F.G., Crist, T.O., Fuller, R.J., Sirami, C., Siriwardena, G.M. & Martin, J.-L. (2011) Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecology Letters*, **14**, 101–112.

Holland, J.M., Birkett, T. & Southway, S. (2009) Contrasting the farm-scale spatio-temporal dynamics of boundary and field overwintering predatory beetles in arable crops. *BioControl*, **54**, 19–33.

Homburg, K., Homburg, N., Schäfer, F., Schuldt, A. & Assmann, T. (2014) Carabids.org - a dynamic online database of ground beetle species traits (Coleoptera, Carabidae) eds C. Dytham & R. Ewers. *Insect Conservation and Diversity*, **7**, 195–205.

Knapp, M. & Knappová, J. (2013) Measurement of Body Condition in a Common Carabid Beetle, *Poecilus cupreus* : A comparison of Fresh Weight, Dry Weight, and Fat Content. *Journal of Insect Science*, **13**, 1–10.

Lee, J.C. & Landis, D.A. (2002) Non-crop habitat management for carabid beetles. *The agroecology of carabid beetles*, 2002nd ed (ed J.M. Holland), p. Intercept, Andover.

Lindroth, C.H. (1985) *The Carabidae (Coleoptera) of Fennoscandia and Denmark*, Fauna entomologica Scandinavica. Brill, Leiden.

Östman, Ö., Ekbom, B., Bengtsson, J., Weibull, A.-C. & Ostman, O. (2001) Landscape Complexity and Farming Practice Influence the Condition of Polyphagous Carabid Beetles. *Ecological Applications*, **11**, 480.

Palmu, E., Ekroos, J., Hanson, H.I., Smith, H.G. & Hedlund, K. (2014) Landscape-scale crop diversity interacts with local management to determine ground beetle diversity. *Basic and Applied Ecology*, **15**, 241–249.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Core Team. (2016) nlme: Linear and Nonlinear Mixed Effects Models, http://cran.r-project.org/web/packages/nlme/

R Core Team. (2015) R: A language and environment for statistical computing, https://www.R-project.org/

Ribera, I., Dolédec, S., Downie, I.S. & Foster, G.N. (2001) Effect of land disturbance and stress on species traits of ground beetle assemblages. *Ecology*, **82**, 1112–1129.

Roduit, N. (2016) JMicroVision: image analysis toolbox for measuring and quantifying components of high-definition images. Version 1.2.2, http://www.jmicrovision.com/

Rusch, A., Bommarco, R., Chiverton, P., Öberg, S., Wallin, H., Wiktelius, S. & Ekbom, B. (2013) Response of ground beetle (Coleoptera, Carabidae) communities to changes in agricultural policies in Sweden over two decades. *Agriculture, Ecosystems & Environment*, **176**, 63–69.

Schellhorn, N.A., Gagic, V. & Bommarco, R. (2015) Time will tell: resource continuity bolsters ecosystem services. *Trends in Ecology & Evolution*, **30**, 524–530.

Straub, C.S., Finke, D.L. & Snyder, W.E. (2008) Are the conservation of natural enemy biodiversity and biological control compatible goals? *Biological Control*, **45**, 225–237.

Symondson, W.O.C. (2002) Diagnostic techniques for determining carabid diets. *The agroecology of carabid beetles* (ed J.M. Holland), p. Intercept, Andover.

Tscharntke, T., Bommarco, R., Clough, Y., Crist, T.O., Kleijn, D., Rand, T.A., Tylianakis, J.M., Nouhuys, S. van & Vidal, S. (2007) Conservation biological control and enemy diversity on a landscape scale. *Biological Control*, **43**, 294–309.

Wallin, H. (1985) Spatial and temporal distribution of some abundant carabid beetles (Coleoptera: Carabidae) in cereal fields and adjacent habitats. *Pedobiologia*, **28**, 19–34.

Wamser, S., Dauber, J., Birkhofer, K. & Wolters, V. (2011) Delayed colonisation of arable fields by spring breeding ground beetles (Coleoptera: Carabidae) in landscapes with a high availability of hibernation sites. *Agriculture, Ecosystems & Environment*, **144**, 235–240.

PUBLICATION LIST

International journal articles included in this thesis

Sirami C., **A. Bosem Baillod***, C. Bertrand*, R. Carrié*, A. Hass*, L. Henckel*, P. Miguet*, C. Vuillot*, A. Alignier, J. Girard, P. Batáry, Y. Clough, C. Violle, D. Giralt, G. Bota, I. Badenhauser, G. Lefebvre, N. Gross, B. Gauffre, A. Vialatte, F. Calatayud, A. Gil-Tena, N. Quesada-Pizarro, L. Tischendorf, S. Mitchell, K. Lindsay, R. Georges, S. Hilaire, J. Recasens, J. Bosch, J. A. Barrientos, A. Ricarte, Mª Á. Marcos, J. Minano, R. Mathevet, A. Gibon, J. Baudry, G. Balent, B. Poulin, F. Burel, T. Tscharntke, V. Bretagnolle, G. Siriwardena, A. Ouin, L. Brotons, J.-L. Martin**, L. Fahrig**. Enhancing biodiversity across taxa and regions by increasing multiple components of agricultural landscape heterogeneity.
**These co-authors contributed equally as part of their PhDs and should be considered co-second authors.*
***These co-authors contributed equally to the project coordination and should be considered co-last authors.*
(in preparation)

Bosem Baillod A.*, A. Hass *, P. Batáry, Y. Clough, C. Sirami, J.-L. Martin, L. Fahrig, A. Alignier, Mª Á. Marcos, J. A. Barrientos, J. Baudry, C. Bertand, G. Bota, V. Bretagnolle, L. Brotons, F. Burel, R. Carrié, G. Lefebvre, R. Georges, B. Gauffre, D. Giralt, N. Gross, S. Hilaire, J. Minano, A. Ouin, B. Poulin, A. Ricarte, A. Saintilan, G. Siriwardena, T. Tscharntke. Configurational and compositional heterogeneity of farmland affect flower-visitor and ground-dwelling arthropod traits across Europe
**Equally contributing authors. (in preparation)*

Bosem Baillod A., Tscharntke T., Péter Batáry, Bertand C., Gross N., Hass A., Sirami C., Martin J.-L., Fahrig L., Violle C., Barrientos J. A., Saintilan A., Baudry J., Bota G., Bretagnolle V., Brotons L., Burel F., Carrié R., Lefebvre G., Georges R., Gauffre B., Giralt D., Hilaire S., Minano J., Ouin A., Poulin B., Siriwardena G., Clough Y. Biological pest control across Europe depend on cascading effects of landscape crop heterogeneity and species traits.
(in preparation)

Bosem Baillod A., T. Tscharntke, Y. Clough & P. Batáry. Cereal aphids, their enemies and biological control are driven by complex interactions between landscape-wide cropland spatial and temporal heterogeneity.
(Submitted to "Journal of Applied Ecology")

Book chapter

Loos J., P. Batáry, **A. Bosem Baillod**, S. Bänsch, I. Grass, A. Hass, J. Rosa & T. Tscharntke. Vulnerability of ecosystem services in farmland depends on landscape structure in *Atlas of Ecosystem Services – Risks and Opportunities* (Eds Klotz S., Bonn A., Seppelt R., Schröter M., Baessler C.), Springer. (*Submitted*)

International conferences and invited talk

Hass A.*, **A. Bosem Baillod**, P. Batáry, C. Sirami & T. Tscharntke. Farmland heterogeneity effects on trait filtering of predatory and flower-visiting arthropod communities across Europe. **Speaking person*
Talk, 46th Annual Meeting of the Ecological Society GfÖ, 2016, Marburg (Germany)

Bosem Baillod A.*, P. Batáry, Y. Clough & T. Tscharntke. Landscape crop heterogeneity affects trophic group structure of carabid and rove beetle communities. **Speaking person*
Poster, 45th Annual Meeting of the GfÖ, 2015, Göttingen (Germany)

Bosem Baillod A.*, P. Batáry, Y. Clough & T. Tscharntke. Relative importance of landscape heterogeneity, crop identity and semi-natural field margins on functional diversity of rove and carabid beetles. **Speaking person*
Talk, IALE World Congress, 2015, Portland, Oregon (USA)

Bosem Baillod A. Can the landscape crop heterogeneity benefit biodiversity and biological control in Europe?
Seminar talk, Centre for Environmental & Climate research, University of Lund, 2016, Lund (Sweden)

Non-scientific talk

Hass A.*, **A. Bosem Baillod***, Teja Tscharntke, Péter Batáry, Yann Clough. Das FarmLand-Projekt: Erste Ergebnisse aus Göttingen (The FarmLand project: First results from Göttingen). **Speaking persons*
Presentation of preliminary project results to farmers, 2014, Göttingen (Germany)

CURRICULUM VITAE

Aliette Bosem Baillod
Georg-August Universität, DNPW Abt. Agrarökologie
Grisebachstr. 6, 37077 Göttingen

Citizenships: French & Swiss
Born 30.12.1987 in Basel (CH)

EDUCATION

Oct. 2013- Jan. 2017	**PhD- Dr. agr. - International agricultural sciences, University of Göttingen (Germany)** *Supervisors*: Prof. T. Tscharntke & Dr. P. Batáry (Uni. of Göttingen); Dr. Yann Clough (Uni. of Lund)
2009-2012	**Msc. Agricultural engineering,** major in Agroecology, **Institut Supérieur d'Agriculture ISARA-Lyon - engineering college (France)**
2009-2011	**Msc. Organic Agriculture** major in Agroecology, **University of Wageningen (Netherlands)**
2006-2009	**Bsc. Agricultural engineering**, **ISARA-Lyon (France**)

RELEVANT WORK EXPERIENCE

Nov. 2012- Oct. 2013	**Research Assistant, University of Göttingen, Dept. of Crop Sciences** *Working group: Agroecology, Prof. T. Tscharntke*
Mar. 2012- Aug. 2012	**Internship, University of Lund, Department of Biology (Sweden)** *Working group: Soil Ecology & Centre for Environmental and Climate research, Prof. K. Hedlund & Prof. H. Smith*
Sept. 11- Dec. 11	**Research Engineer, ISARA-Lyon** *Working group: Agroecology & Environment, Dr. C. David & Dr. A. Wezel*
Feb. 11- Aug. 11	**Msc Thesis**, **ISARA-Lyon & University of Wageningen** *Supervisors: Dr. A. Wezel & Dr. W. Rossing*
March 10- Aug. 10	**Internship, University of Wageningen, Dept. of Plant Sciences** *Working group: Organic Farming Systems & Soil Quality, Dr. J. Scholberg & Dr. M. Pulleman*

COMPETITIVE GRANTS

Oct. 2013- Oct. 2016	**PhD scholarship award** from the German Academic Exchange Service (DAAD) for foreigners
July 2015	**Travel grant** from Göttingen International (Uni. of Göttingen) to the Int. Association for Landscape Ecology IALE World Congress, Portland, USA

ACKNOLEDGEMENTS

I first express my gratitude to my supervisors Prof. Teja Tscharntke, Dr. Yann Clough and Dr. Péter Batáry for giving me this unique opportunity to complete my PhD studies in the Agroecology group. Many thanks to Teja for the great support and the nice discussions we had all these years. I am grateful to Yann who supported me from far away in Sweden. It was always nice to get quick answers to all issues I had and to get new ideas to see the forest through the trees. A special thank you goes to Péter, who was my daily support in all matters and who involved me in a lot of academic activities beside the PhD project. I also thank Prof. Stefan Vidal for joining my PhD committee and for writing the yearly recommendation letters for the scholarship applications.

I am especially grateful to Annika Haß. Together we managed the FarmLand project here in Göttingen, we worked hard but we laughed a lot as well. Thank you for the nice team-work, your calmness and patience in all situations. I am also indebted to our numerous "HiWis" and students who helped us in the field and the lab. A special thank you goes to Brigitte Jünemann who helped out in field-work preparation and in the lab, Aline Marcastel who took care of the predation experiments in the second year, Tessa Bornemann and Sarina Kivelitz, who both worked on measuring intra-species trait variability. The complete FarmLand team and especially the "FarmLand-girls" are thanked for the great work we achieved and the numerous nice adventurous trips we did. It was so great to discover nice places in France and Spain.

All colleagues from the Agroecolgy group are thanked here for the very nice working atmosphere, for all the fruitful discussions and for their help when I needed it.

I am greatly indebted to my family. Especially Stefan for his unconditional emotional support and my parents for supporting me during my studies, which were all so far away from home. A special thank you goes to Yeshua for guiding my steps forward.

Last but not least, I thank the DAAD (Deutscher Akademischer Austauschdienst), the BMBF (Bundesministerium für Bildung und Forschung) and the BiodivERsA network for financial support. This support can't be guaranteed without the many German and other European tax payers. I thank them for unconsciously contributing to move science forward.